EVOLUTIONARY MODELS FOR THE ORIGINS OF AGRICULTURE

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Declaration of Ownership

I, Elizabeth Gallagher, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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Abstract

The transition from hunting and gathering to farming at the end of the Pleistocene was one of the most important events in human history, having major impacts on human demography, evolution, health, culture, technology, and social stratification. The reasons why some societies switched to farming are still debated, with climate stabilisation and population pressure as popular hypotheses. However, since these processes occurred so long ago, investigating the transition can be difficult without the use of mathematical models.

In this thesis I investigate the effect of various factors, including population size, conservatism, property rights, environmental conditions, climate variability, and mobility, on the transition to farming using evolutionary models. I do this by implementing an intensive parameter sensitivity analysis method on an existing game theoretical model (Bowles and Choi, 2013) for the origins of agriculture, and also develop and explore my own agent-based models of social and environmental interactions.

Using the Bowles and Choi model, I find that the key parameters for the emergence of farming are group structuring, group size, conservatism, and farming-friendly property rights. The analysis of this model also shows that although advantageous, it is not essential for the emergence of farming for farming productivity to be greater than foraging productivity. In the development of my own model, I first consider mobility changes in a forager population, and find that low depletion and high growth rates can lead to reduced mobility, low fitness, and high population density. When I add subsistence behaviours to the model I find that three behaviours can evolve in response to different environmental conditions; mobile foraging, sedentary foraging, and sedentary farming. I also find a relationship between reduced mobility, the emergence of farming, decreased fitness and high population densities. Additionally, my model predicts that population pressure was caused by, but not causal of, the switch to farming. Importantly, these results concur with the observed archaeological data and ethnographic record, and highlight the value of using modelling to validate and/or challenge observed data.

Acknowledgements

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Contents

6 Mobility and Subsistence Strategy Changes in a Mixed Population 193

7 Conclusions 239

List of Figures

List of Tables

Glossary

Agriculture Farming dominates the activities and contributes the majority of the diet of a group.

Broad Spectrum Revolution (BSR) Increases in the diet breadth of foragers before the transition to agriculture.

Cultivation Intentionally preparing the soil for planting wild or domesticated plants.

Cultural Evolution Applying evolutionary theory to cultural traits (instead of genes) to understand cultural change (as opposed to genetic change).

Culture Information acquired via social transmission which is capable of affecting individual behaviour.

Domestication Morphological or genetic changes in plant and animal species due to selective breeding by humans.

Farming Cultivating domesticated plants and/or raising domesticated animals for food.

Foraging Obtaining wild plants and/or wild animals for food, also referred to as ‘hunting and gathering’.

Human behavioural ecology (HBE) A framework in which to study diversity in human behaviour in the context of adaptive solutions to the environment, i.e. fitness-optimising behaviours being selected for.

Hunter-Gatherer A person who obtains most of their food by foraging.

Logistical Mobility The movement of smaller groups away from and back to their base camp.

Neolithic demographic transition (NDT) The increase in fertility rates seen during the transition to agricultural economies.

Niche construction Environmental modification by organisms, which can in turn change selection pressures.

Optimal Foraging Theory (OFT) A framework for understanding how animals forage for food by minimising costs.

Residential Mobility The movement of an entire group to a different camp.

Sedentism Where a group at least partially remains at the same location year-round.

Subsistence strategy The manner in which food is obtained by a group. This could include foraging or farming, or a blend of both.

1

Introduction

Summary

After around 190,000 years of anatomically modern humans living as hunter-gatherers, societies began to make a transition to agricultural subsistence systems. These transitions are thought to have occurred independently in several regions of the world between 11,500 and 3,500 years before present (yBP) (Bellwood et al., 2005). Farming has spread to most of the world from these centres. This transition had major impacts on human demography, evolution, diet, health, culture, technology, and social inequality (Diamond, 2002; Fuller, 2010; Lambert, 2009; Starling and Stock, 2007). It is generally agreed that there are at least three separate regions around the world where agriculture originated independently: southwest Asia, Mesoamerica, and China (Bellwood et al., 2005; Diamond, 2002; Fuller, 2010). There is also growing evidence for additional independent origins of domestication, which include the Eastern United States, the Andes, the Central and South America tropics, New Guinea, West Africa, and southern and northern India (Fuller, 2010). A range of different explanations for the development of agriculture have been proposed, including those based on climate changes and population pressure.

Whereas the long-term advantages of farming are clear in that it is a strategy that has generally led to increased carrying capacities and greater reproductive successes (Bocquet-Appel, 2011b), the short-term fitness payoffs are less obvious, as Diamond (2002, p. 700) observes:

> The question 'why farm?' strikes most of us modern humans as silly. Of course it is better to grow wheat and cows than to forage for roots and snails. But in reality, that perspective is flawed by hindsight. Food production could not possibly have arisen through a conscious decision, because the world's first farmers had

> around them no model of farming to observe, hence they could not have known that there was a goal of domestication to strive for, and could not have guessed the consequences that domestication would bring for them. If they had actually foreseen the consequences, they would surely have outlawed the first steps towards domestication, because the archaeological and ethnographic record throughout the world shows that the transition from hunting and gathering to farming eventually resulted in more work, lower adult stature, worse nutritional condition and heavier disease burdens.

Investigating the reasons behind the transition to agriculture is challenging because modern ethnographic data may not be informative on ancient population dynamics, and the material culture record is sparse and only weakly informative on social aspects of the transition. Furthermore, the appearance of domestication traits in various species is likely to postdate their initial cultivation or management, sometimes by a considerable margin (Zeder, 2008). In this context, mathematical models can be helpful in exploring the ecological and social conditions necessary for the transition to agriculture. There are many examples of such models (e.g. Bowles and Choi (2013); Dow and Reed (2011); Dow et al. (2009); Locay (1989); Marceau and Myers (2006); Reynolds (1986); Richerson et al. (2001); Winterhalder and Goland (1993); Wirtz and Lemmen (2003)), which, together, have explored most of the major hypotheses for the origins of agriculture.

However, many of the existing models are lacking important components, are analysed using ill defined parameter values, and/or do not include social-environment interactions. Furthermore, the strong relationship between mobility, population density and the origins of farming has only been specifically studied in very few models. Hence the purpose of this thesis is to two-fold; the first is to implement a more thorough parameter analysis method on an existing model for the origins of agriculture, and the second is to build a mathematical model which specifically considers how mobility and population density are interlinked with the origins of agriculture.

In this first chapter I will introduce the topic of the thesis – the origins of agriculture. By reviewing archaeological evidence, I will build a picture of the factors leading up to and surrounding the switch to agriculture, and the immediate implications, both locally and globally. Since the transition to agriculture in SW Asia has received more attention in the literature than in other parts of the world, my discussion will focus mostly on this area, and then I will give a brief comparison to some of the origins in other parts of the world. I will then briefly review the genetic evidence for the spread of farming into Europe in Section 1.2. In Section 1.3 I will look at factors which may have been important for the transition to agriculture, and discuss how human behavioural ecology

(HBE) can be a useful framework for understanding the transition. Since decreased mobility is one of the key correlates of the switch to farming, in Section 1.4 I will discuss hunter-gatherer mobility. I will finish this chapter with a discussion of the structure and aims of the thesis.

1.1 The Origins of Agriculture and the Effects

Agriculture has been argued to have originated independently in at least three separate regions: SW Asia, Mesoamerica and in China (Bar-Yosef, 1998; Brown et al., 2006). Fuller (2010) also states that there is evidence for the independent domestication of various species in the Eastern U.S, the Andes, the Central and South America tropics, New Guinea, West Africa, Japan, Tibet, and India. Figure 1.1 gives these proposed independent origins and the crops which would have been cultivated and animals domesticated.

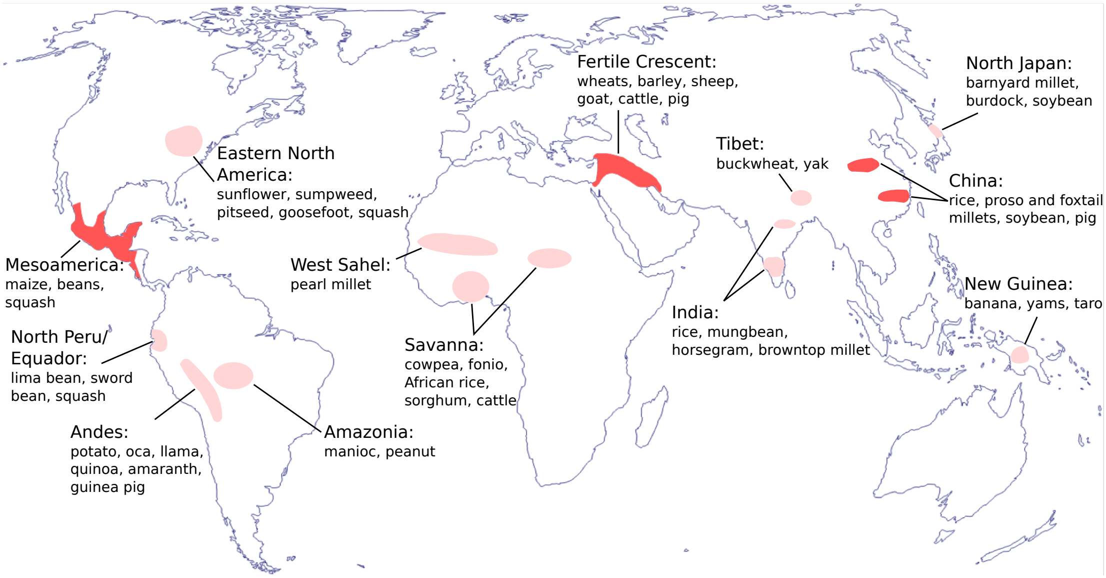
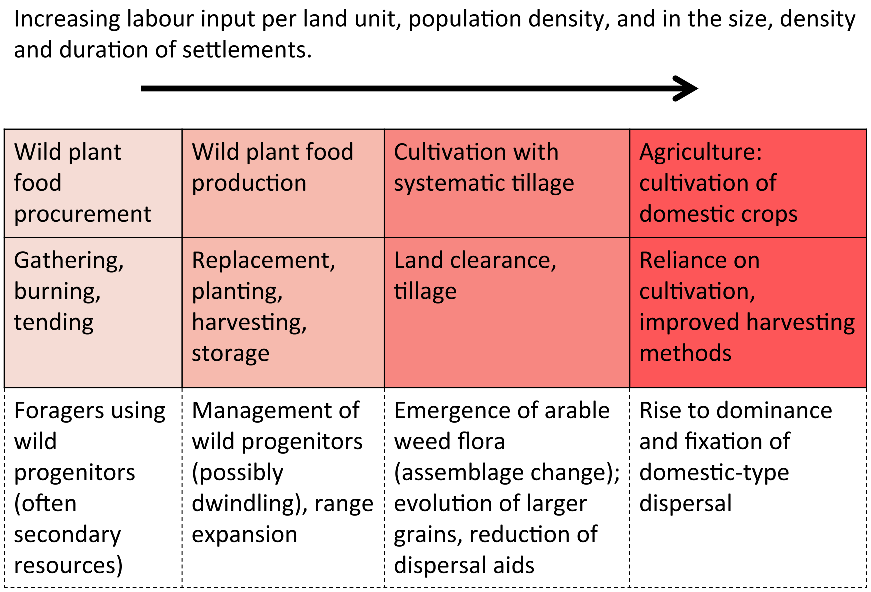


Figure 1.1: Proposed independent centers of domestication, with the most widely accepted regions shown in dark red. The crops cultivated at each centre are also given. Adapted from (Fuller, 2010).

Archaeological evidence for agriculture can come from the presence of the morphological traits or genetic variants associated with domestication (Zeder et al., 2006), and evidence for cultivation before domestication can be seen by the presence of weed seeds which would have grown with the crops (Willcox et al., 2008) and also by crop-processing by-products (Fuller et al., 2012). A summary of the changes in plant food procurement from foraging to agriculture, and the associated types of archaeobotanical evidence found, are shown in Figure 1.2. Using this evidence it can be seen that the timings for early cultivation and the speed of development to a fully agricultural economy, are quite different for each of the main regions for independent origins of agriculture – these are given in Table 1.1.



Increasing labour input per land unit, population density, and in the size, density and duration of settlements.

Wild plant food procurement	Wild plant food production	Cultivation with systematic tillage	Agriculture: cultivation of domestic crops
Gathering, burning, tending	Replacement, planting, harvesting, storage	Land clearance, tillage	Reliance on cultivation, improved harvesting methods
Foragers using wild progenitors (often secondary resources)	Management of wild progenitors (possibly dwindling), range expansion	Emergence of arable weed flora (assemblage change); evolution of larger grains, reduction of dispersal aids	Rise to dominance and fixation of domestic-type dispersal

Figure 1.2: Stages from foraging to agriculture (left to right) with the associated expectations in the archaeobotanical evidence (bottom row). Adapted from Figure 1 in Fuller (2007).

The transition to agriculture in SW Asia has been studied extensively for many years, and therefore the literature is more detailed than for other parts of the world. Because of this, in this section I will focus on building a picture of societal and climate changes before and during the transition to agriculture in SW Asia. I will then give a brief review of the transition in other parts of the world to illustrate how a worldwide narrative for the transition does not hold. Since there is a notable amount of literature for the transitions in China, Mesoamerica, and eastern North America (ENA), these will be the areas I look at.

Definitions of terms relevant to this thesis are given in the glossary on page 20. I use terms such as ‘the origins of agriculture’ and ‘the transition/switch to agriculture’ to refer to the period of time from when people first began to cultivate to when these people fully adopted an agricultural economy, without having copied these behaviours from existing farmers.

1.1.1 The Origin of Agriculture in Southwest Asia

The transition to agriculture from hunting and gathering is thought to have first begun at the start of the early Holocene around 11,500 years before present (yBP) in SW Asia (Zeder, 2011, this area is shown in Figure 1.3). But perhaps it is from the Late Upper

Table 1.1: Approximate timings for the earliest cultivation evidence and the full adoption of agriculture in the main regions of agricultural origins.

Region	**Early cultivation**	**Agricultural economy fully adopted**	**Difference**
SW Asia	Rye: 11,500 BP (Zeder, 2011)	8000 BP (Zeder, 2011)	3500 years
Southern China - Yangtze River areas	Rice: 10,000 BP (Jiang et al., 2006)	4300-5300 BP (Zhao, 2011)	4700-5700 years
Northern China - Yellow River area	Millet: 10,000 BP (Lu et al., 2009)	7000-6000 BP (Zhao, 2011)	3000 - 4000 years
Mesoamerica	Maize: 8700 BP (Ranere et al., 2009)	3500-2900 BP (Barker, 2006, p. 251)	5200 - 5800 years
Eastern North America	Squash: 5000 BP (Smith, 2011)	1300 BP (Zeder and Smith, 2009)	3700 years

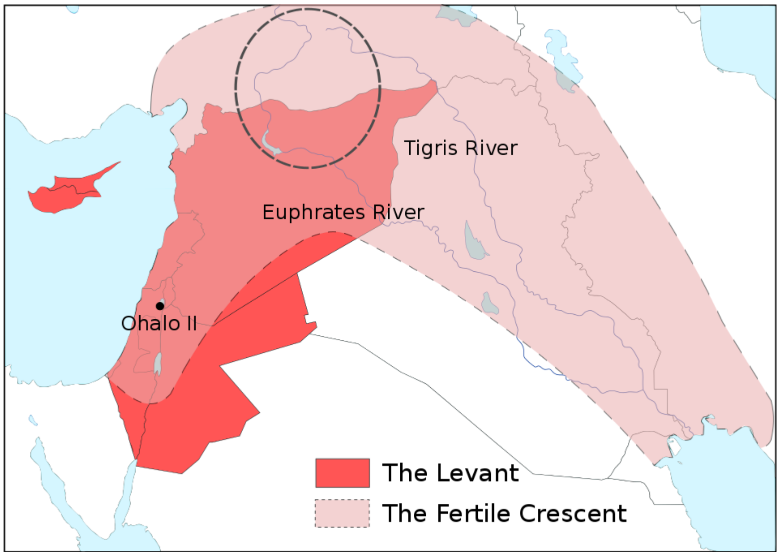


Figure 1.3: SW Asia. The Levant in shown in red, the Fertile Crescent in pink and the ‘core area’ of SW Asian plant domestication is within the dashed line.

Table 1.2: Approximate dates for archaeological periods in SW Asia. Unless otherwise stated dates are given in cal BP.

Archaeological/cultural period	Start cal BP	End cal BP	Reference
Kebaran	21,250	17,575	Goring-Morris and Belfer-Cohen (2011)
Early-Late Epi-Palaeolithic	24,000	11,600	Goring-Morris and Belfer-Cohen (2011)
Natufian	14,900	11,750	Goring-Morris and Belfer-Cohen (2011)
Khiamian	12,175	11,800	Goring-Morris and Belfer-Cohen (2011)
Pre-Pottery Neolithic A (PPNA)	11,800	10,500	Conolly et al. (2011)
Early PPNB	10,500	10,300	Conolly et al. (2011)
Middle PPNB	10,300	9500	Conolly et al. (2011)
Late/Final PPNB	9500	8800	Conolly et al. (2011)
Pre-Pottery Neolithic C (PPNC)	8800	8400	Conolly et al. (2011)
Khirokitian	7000 cal BC	5500 cal BC	Colledge et al. (2004) and personal communication from Colledge
Early (Pottery) Neolithic (EN)	8400	7500	Conolly et al. (2011)

Palaeolithic/Early Epi-Palaeolithic that the very first processes leading to the transition can be traced (Goring-Morris and Belfer-Cohen, 2011). Archaeological/cultural periods mentioned in this section are shown in Table 1.2.

In the Upper Palaeolithic, hunter-gatherer groups in SW Asia were highly mobile and mostly relied on small to medium sized ungulates. In the Epi-Palaeolithic there is evidence for subsistence intensification, where more effort was spent getting more nutrients from the environment (Munro, 2009). People started to include previously ignored, low-ranked species into their diets – smaller mammals, birds, fish, tortoises, crabs, small-grained grasses, ember wheat and barley (Flannery, 1969; Weiss et al., 2004). This increase in the dietary breadth before the transition to agriculture is known as the Broad Spectrum Revolution (BSR).

It has been proposed that during the early and middle Epi-Palaeolithic mobile-band groups were made up of around 25 individuals, with around 250-500 needed for sustainable mating networks (Goring-Morris and Belfer-Cohen, 2011). Due to the Last Glacial Maximum populations would have been packed into refugia (such as Ohalo II on the shore of the Sea of Galilee in Israel), and hence population densities increased.

The slight climate amelioration at the end of the Late Glacial Maximum (around 15,000 yBP) saw the emergence of less mobile foragers, the Early Natufian (Zeder and

Smith, 2009). Bellwood et al. (2005) notes a large increase in settlement size and Bocquet-Appel and Bar-Yosef (2008) infer an increase in population size, during the transition from the Kebaran to the early Natufian. With the Natufian culture there is also evidence for pit houses, stone structures, storage pits, symbolic behaviours, burial grounds, jewellery, decorated items and technological innovations, such as sickles, in the archaeological record (Belfer-Cohen and Goring-Morris, 2011; Boyd, 2006). Belfer-Cohen and Goring-Morris (2011) suggest that these characteristics could only have occurred because of social mechanisms to keep groups together; for example, emerging social and community identities, territoriality and competition. Hunting and gathering was intensified with the Natufians, and there is evidence for increased preparation and processing of foods (Goring-Morris and Belfer-Cohen, 2011).

During the abrupt cold and dry period of the Younger Dryas (12,900 to 11,700 yBP) (Broecker et al., 2010) societies in the Southern Levant appear to have become mobile again, whilst societies in the Euphrates valley and the Zagros stayed semi-sedentary (Zeder and Smith, 2009). The Younger Dryas was followed by a return to wet and warmer conditions, with the expansion of woodland and parkland, in the Holocene (Bar-Yosef, 1998). It is during this climate reversal that sedentism across the Fertile Crescent became possible (due to these climate changes being advantageous for annual cereals) and the first evidence of cultivation appeared (Zeder and Smith, 2009). Hence, the transition from hunter-gathering to cultivation co-occurred with these late-Pleistocene environmental changes (Moore and Hillman, 1992; Willcox et al., 2009), leading to many theories (see subsection 1.3.1) that the Younger Dryas and/or climate amelioration in the Holocene had a strong effect on the development of agriculture.

In the Pre-Pottery Neolithic A (PPNA), from around 11,600 yBP, there is evidence for a large increase in population size, settlement size, social organisation, exchange networks, reduced residential mobility, accumulation of surpluses and a hierarchy of site sizes (Belfer-Cohen and Goring-Morris, 2011). Later, in the Pre-Pottery Neolithic B, beginning at around 10,500 yBP, large permanent village societies emerge and there is an increasing dependence on domesticated species (Bellwood et al., 2005; Goring-Morris and Belfer-Cohen, 2011). By 9000 yBP farming is generally believed to have become well-established (Conolly et al., 2011), and by around 8000 yBP it is suggested that human populations all over the Fertile Crescent relied on an agricultural economy with fully domesticated resources (Zeder, 2011). Therefore it took around 3500 years for the transition from the initial cultivation of rye to an agricultural economy.

The eight crops which are associated with early agriculture in SW Asia – the ‘founder crops' – are emmer wheat, einkorn wheat, barley, lentil, pea, flax, chickpea and bitter vetch (Zohary, 1996). These species, along with sheep, goats, cattle and pigs (Zeder, 2008), are thought to have been initially domesticated in the Fertile Crescent, and the wild ancestors of these are still found in this region today.

1.1.2 Other Independent Transitions

Figure 1.4: Early millet (triangles) and rice (circles) cultivation sites in China along the Yellow and Yangtze rivers respectively. Adapted from Zhao (2011).

Beginning with SW Asia, the first steps towards agriculture took place at least 1000 years apart in each of the three major centres for the origins of agriculture. Furthermore, the transition from some cultivation (beginning with plant cultivation) to a fully agricultural economy took different amounts of time (see Table 1.1).

In northern China, foxtail and broomcorn millet were the initial crops, with millet cultivation becoming established by 7500 yBP[1] in the Yellow River basin (Fuller, 2010), and by 7000 to 6000 yBP full millet farming-based subsistence had been adopted (Zhao, 2011). In the middle and lower Yangzte regions the cultivation of rice may have begun as early as 10,000 yBP (Jiang et al., 2006), with domestication occurring around 6000 yBP[2] (Fuller et al., 2007), rice cultivation becoming established by 7000 yBP[3] (Fuller et al., 2007), and full rice agriculture becoming established at around 6400 to 5300 yBP and 5200 to 4300 yBP in the middle and lower Yangtze River regions respectively (Zhao, 2011) (see Figure 1.4 for these regions). Although, due to the large amount of

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[1] 5500 BC in Fuller (2010) [2] 4000 BC in Fuller et al. (2007) [3] 5000 BC in Fuller et al. (2007)

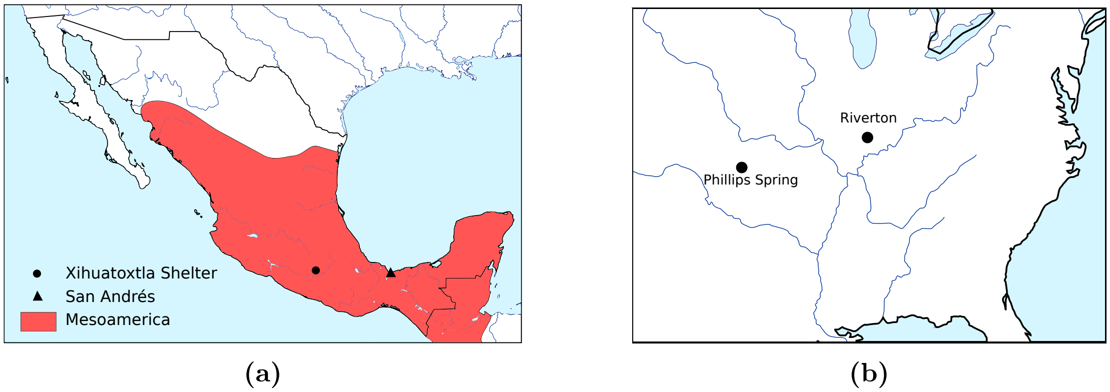

Figure 1.5: Mesoamerica and eastern North America. (a) Mesoamerica and sites of early cultivation. Adapted from Piperno (2011). (b) Eastern North America and sites where the earliest evidence of domesticated plants are found. Adapted from Smith (2011).

information exchange between the different regions in China, Cohen (2011) suggests that it still needs to be assessed whether rice- and millet-based agricultural systems could have arisen truely independently from one another. Hence the full transition occurred over around 3000-4000 years in northern China, and around 4700-5700 years in the Yangzte regions.

In Mesoamerica, the transition to mostly relying on farming from mostly foraging took 5200-5800 years – longer than in other parts of the world (Barker, 2006). The Mexican western lowlands have been suggested to be the site for the domestication of maize (Barker, 2006), and the earliest record for the cultivation of maize dates to 8700 yBP from Xihuatoxtla Shelter in the Central Balsas River Valley (Ranere et al., 2009) (see Figure 1.5a). Domesticated avocado and some squash species have been found in sites which date to 9000-7000 yBP[4], and at sites dating from the Coxcatlan phase (5000-4300 BC) there is evidence of domesticated beans, gourds, some other squash species and chilli (Barker, 2006). It is not until the Ajalpan phase from 3500-2900 yBP[5] that there is evidence for sedentary village life based on farming (Barker, 2006).

In eastern North America (ENA) (see Figure 1.5b) the earliest evidence for cultivation is of pepo squash in Illinois, dating from 5025 calibrated calendar (cal) years BP (Smith, 2011). Squash, sunflower, marsh elder, and two species of chenopod were first brought under domestication from about 5000 to 3400 years ago (Smith, 2006). By 3800 yBP there is evidence of a crop complex composed of these five species (Smith and

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[4] 7000-5000 BC in Barker (2006)

[5] 1500-900 BC in Barker (2006)

Yarnell, 2009), but perhaps only by 700 AD is there evidence for a fully agricultural economy (Zeder and Smith, 2009). Thus the ENA transition was the latest and took around 3700 years.

By at least the Early Neolithic (around 9000 yBP), there is evidence for sedentary village life, with storage, ritual, and burials, in the low altitude regions of China – along the yellow river in northern China, and the Middle and Lower Yangtze (Cohen, 2011). Likewise, in ENA the first evidence for early cultivation and domestication are seen in small and more sedentary settlements in resource-rich river valley environments (Smith, 2011), with little evidence for social hierarchy (Zeder and Smith, 2009). Thus in SW Asia, China and ENA agriculture started and developed in sedentary settlements near to river valleys. In contrast, in Mesoamerica many of the sites where agriculture started were smaller, seasonally occupied and mostly in rock shelters near seasonal streams (Piperno, 2011).

As in SW Asia, populations in China and ENA were found to have increased before domestication began (Cohen, 2011; Weitzel and Codding, 2016), although Smith and Yarnell (2009) suggest an absence of carrying-capacity challenges at one of the ENA sites (Riverton). In Mesoamerica there is evidence that population sizes were small before farming began (Ranere et al., 2009), although this is not contradictory to there being carrying-capacity challenges.

In SW Asia climate changes associated with the end of the Pleistocene were correlated with the timings of various changes in behaviour (e.g. changes in mobility and cultivation). During the Pleistocene-to-Holocene transition (around 12,800 to 11,600 yBP) in China there were localised environmental changes, with changes in monsoon cycle intensities in the north, and more stable, warmer, wetter and resource-abundant in the south (Cohen, 2011). In northern China these changes promoted people to retreat to more favourable sites where they established less mobile and larger communities, and eventually began to cultivate (Bar-Yosef, 2011). In southern China hunting and gathering persisted for much longer and the impact of climate change is less clear. At the end of the Pleistocene in the Americas (around 11,400 yBP) the climate became significantly wetter and warmer with a shift from savanna-like vegetation to tropical forest (Piperno, 2011). However, here there was still a significant delay before early cultivation attempts occurred. Likewise, early cultivation in ENA occurred much later than the beginning of the Holocene, but here it is suggested that later climate changes may have played a part in changes to human behaviour. Zeder and Smith (2009) suggested that a change in climate 7,000 to 6,500 years ago in eastern North America (ENA) promoted the development of river valley regimes and their enriched floodplains. It was then in these environments where societies became more sedentary and first began to cultivate crops (Smith, 2011). Thus, end of Pleistocene climate changes were most clearly correlated with changes in behaviour in SW Asia and northern China, but less so with southern China, the Americas and ENA.

1.1.3 The Consequences of Agriculture

There are a number of lasting lifestyle changes which occurred before, during and after the transition to agriculture (a few of which are mentioned in the preceding paragraphs). Many of these are interlinked and feedback onto one another, and it is often not clear whether they are causal of, or caused by a switch to farming. In this section I will discuss these changes, their connectivity to one another and implications.

The Broad Spectrum Revolution

Before agriculture was fully adopted there is evidence for a change in subsistence systems – from one based on low-cost resources (e.g. large, slow mammals), to a more labour-intensive system with increased diversity. As mentioned in the previous section this increase in diet breadth is referred to as the broad spectrum revolution (Flannery, 1969).

Sedentism

A key shift during the transition to agriculture was the switch from communities being highly mobile to more sedentary, which in some places occurred before farming began and in others after (Diamond, 2002). However, as I will discuss in Section 1.4, decreased mobility is not always linked with farming, and can also be present in foraging societies.

In the archaeological record sedentism can be seen by the presence of certain items. If a site is occupied year round then there might be evidence of a species from each of the four seasons, e.g. seeds from fruits that are only edible in one season, for each of the seasons. Also, certain commensal species (e.g. mice) thrive around humans, so evidence of their presence can indicate that settlements were lived in for large amounts of time. Other evidence for sedentism includes investment in building large structures, and increases in burials (since all deaths would occur in a similar location) and storage (Dow and Reed, 2015).

Sedentism is linked with several of the other lifestyle changes, which will be discussed in turn in the next paragraphs.

Population Growth, Health, and Quality of Life

An increase in fertility rate leading to higher rates of population growth is seen during the transition to agriculture; this is referred to as the Neolithic demographic transition (NDT) and can be measured by increases in the proportions of juvenile skeletons in cemeteries Bocquet-Appel (2011a). Explanations for this could be that sedentary life allowed for shorter birth intervals, as reduced mobility allows for increased energy for reproduction (Page et al., 2016), or that in more mobile societies having more than one young child would be difficult to carry (Lee, 1979); and another explanation is that there was an increase in fertility due to high calorie foods (Bocquet-Appel, 2011b).

Despite increased fertility rates, there is evidence for a health decline (seen by a decrease of human stature) during the agricultural transition (Cohen, 2009; Lambert, 2009). This could be explained by the negative effects of sedentism and large communities (and hence crowding), for example increased infection, disease and parasites (Cohen, 2009). Bowles (2011) also estimates that the productivity, in terms of caloric returns per amount of labour, of the first farmers is less than it is for foragers in the early Holocene. Furthermore, the amount of work effort may have increased during the transition to agriculture (Haviland, 1996).

Property Rights and Storage

During the transition to agriculture there is evidence for an increase in storage facilities (Bogaard et al., 2009), beginning with communal storage areas and then indoor private storage rooms (Flannery, 2002). Since mobile groups have to move all their belongings with them (a costly process), staying in one place makes storage easier. The accumulation of food reserves reduces risk in times when food is scarce, which further reduces the need for mobility (Testart et al., 1982).

As Winterhalder and Kennett (2009) point out, storage raises issues associated with private property ownership such as defence and the respect of other people's property. Risk reduction for hunter-gatherers may come in the form of sharing, but for sedentary foragers or farmers it may be a better strategy to establish private property and its associated rights (Shennan, 2011).

Social Inequality and Wealth Transmission

Social inequality also became more pronounced during the transition to agriculture (Bowles et al., 2010), with foraging societies perhaps having enforced egalitarianism

(Boehm et al., 1993) – although there is still some evidence for social inequality in foraging societies (e.g. Vanhaeren and d'Errico (2005); Wengrow and Graeber (2015)). Social inequality can be seen in the archaeological record by the presence or absence of grave goods, indicators of storage and nutrition, ceremonial objects and the size and location of dwellings (Bowles et al., 2010). Shennan (2011) estimates a Gini coefficient [6] of 0.4 in pastoralist societies, 0.51 for agriculturalists and 0.19 for hunter-gatherers. As Winterhalder and Kennett (2006, p. 2) remark:

> Agriculture is the precursor, arguably the necessary precursor, for the development of widespread social stratification, state-level societies, market economies, and industrial production (Diamond 1997; Zeder 1991). Social theory (e.g., Trigger 1998) maintains that present-day notions of property, equality and inequality, human relationships to nature, etc., are shaped, at least in part, by the social organization, technology, or food surpluses entailed in our dependence on agriculture.

Bowles et al. (2010) argue that key to the emergence and persistence of social inequality is how wealth is transmitted inter-generationally. For foraging societies it is thought that the transmission of material wealth (e.g. land, livestock) is less important than the transmission of embodied wealth (e.g. nutritional investment) or relational wealth (e.g. social contacts) through generations, and this is perhaps because of the effect mobility has on wealth accumulation (Smith et al., 2010). Hence, perhaps it was only when people began to farm, became more sedentary and stored private property, that material wealth accumulated and social inequality was able to emerge. In fact, Olsson and Hibbs Jr (2005) find that current wealth distribution is strongly correlated with the location and timings of agricultural origins.

The transition from small egalitarian to larger despotic groups could have occurred voluntarily (rather than by force) when there were surplus resources leading to demographic expansion, and also when there were high dispersal costs (Powers and Lehmann, 2014). These conditions are likely to have been met during the Neolithic transition.

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[6] Where a Gini coefficient of 0 indicates complete equality and a value of 1 indicates complete inequality.

1.2 The Spread of Agriculture into Europe

Although this thesis is concerned with the independent origins of agriculture, the spread of agriculture from these origins is also widely studied. Thus for completeness I will discuss the spread of farming from SW Asia into Europe and the contribution the study of genetics has made.

There is evidence for the initial spread of agriculture from SW Asia into Cyprus from around 10,600 years ago (Vigne et al., 2012), then through the Balkans, Central Europe and the West Mediterranean (Olivieri et al., 2013) before finally reaching the British Isles at around 6000 yBP[7] (Stevens and Fuller, 2012). Figure 1.6a shows the earliest dates of archaeological evidence for the Neolithic package of crops and animals across Europe.

Although the routes of spread can be estimated, the mechanisms of the Neolithic transition across Europe is still debated in archaeology, anthropology, and human population genetics, with arguments mostly divided between two contrasting views. Some researchers support the idea that agriculture was introduced into hunter-gatherer communities by the movements of people, where indigenous groups were replaced by or reproduced with the new farming populations. The other argument suggests indigenous hunter-gatherer groups imitated agricultural techniques by a process of cultural transmission from contact with agropastoral communities. These two extreme processes are termed ‘demic diffusion’ and ‘cultural diffusion’ respectively.

If the cultural diffusion model is correct it might be expected that there would be very little genetic footprint from SW Asia in modern Europeans, and hence the current genetic pool should mainly be derived from indigenous European hunter-gatherers. Alternatively, if the demic diffusion model is correct it may be expected that SW Asian Neolithic ancestry would be more pronounced in early farmer and modern European populations (Haak et al., 2010). However, other processes (such as the degree of admixture and other demographic events) during the expansion make this expectation tentative (Rasteiro and Chikhi, 2013).

Hence, to investigate which of the models for the Neolithic transition in Europe is most likely, genetic data can prove extremely useful. Much of the work done on this aims to find out how much of a genetic contribution early SW Asian Neolithic farmers made to modern Europeans.

Ammerman and Cavalli-Sforza predicted that if the demic diffusion model was cor-

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[7] 4000 cal BC in Stevens and Fuller (2012)

rect there would be genetic gradients from the mixing of Neolithic and Mesolithic populations, with the more extreme gene frequencies closest to SW Asia (Ammerman and Cavalli-Sforza, 1973). Menozzi et al. (1978) demonstrated such a cline by using principal component analysis (PCA). The first principal component of variation in modern European allele frequencies from 38 independent alleles (blood groups, the tissue antigen HLA system and some enzymes) from ten loci accounted for 27% of the total variation and was used to generate a synthetic gene map (Figure 1.6b shows their results). However, such PCA patterns could arise through other demographic processes (Novembre and Stephens, 2008).

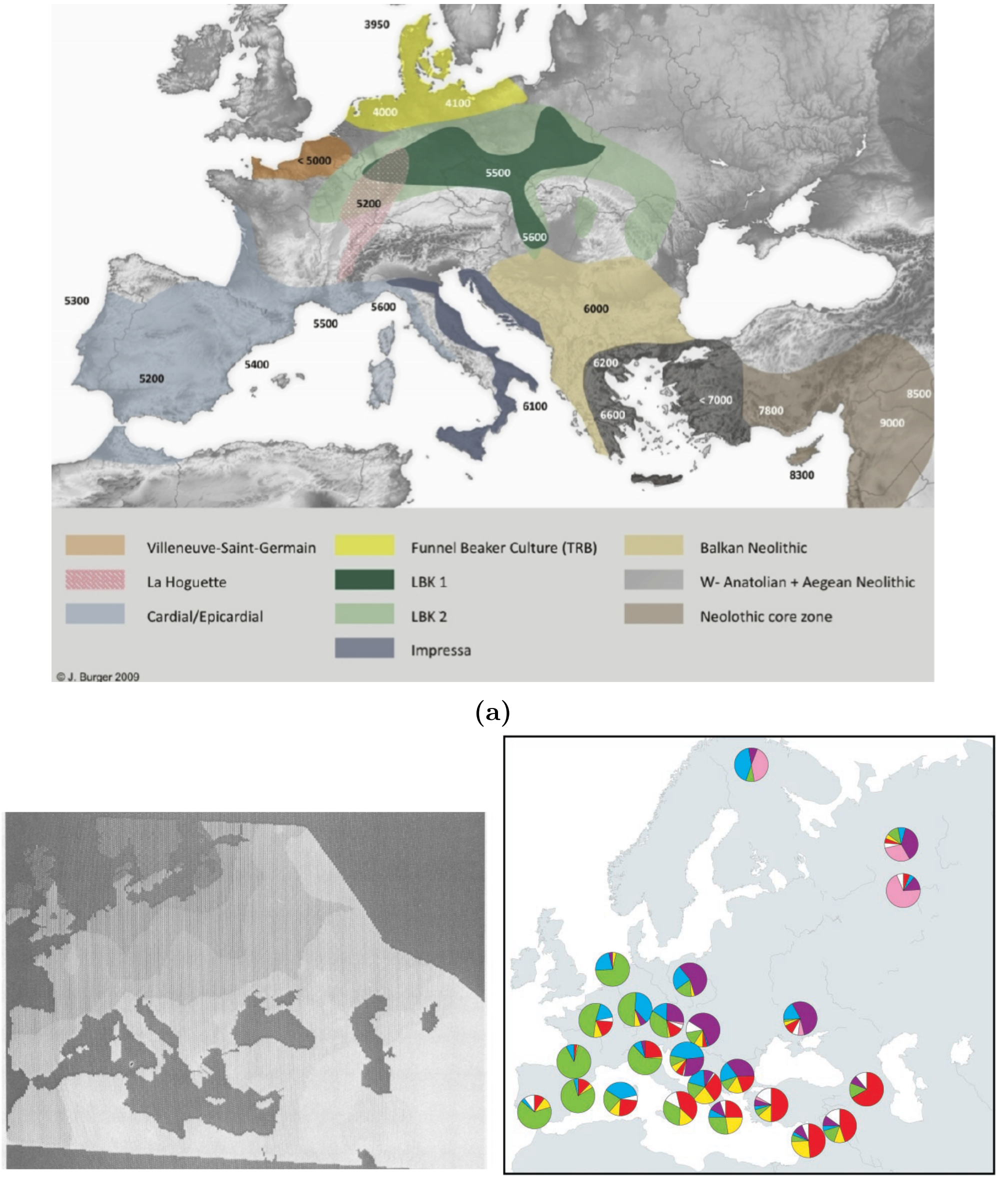
Hence, while this early genetic work was widely interpreted as fitting with the demic diffusion model of a Neolithic wave of advance from SW Asia, where modern Europeans were influenced genetically by SW Asian populations, it did not in itself demonstrate demic diffusion of farmers. However, since then molecular genetic approaches have revealed contrasting and contradictory results concerning the Neolithic contribution to the gene pool of modern Europeans (Haak et al., 2010).

The distribution of mitochondrial DNA (mtDNA) or Y-chromosome haplotype frequencies has been used to infer the movement of females or males respectively. Work on this by Semino et al. (2000) is shown in Figure 1.6c.

The predicted Neolithic genetic contribution to modern Europeans has been seen to vary, from some authors suggesting very little (Haak et al., 2005), others suggesting around 20% (Richards et al., 2000; Semino et al., 2000) or 50% (Chikhi et al., 2002), to others suggesting a majority (Balaresque et al., 2010; Sampietro et al., 2007). Authors have sometimes interpreted little genetic contribution as supporting a cultural diffusion model of the Neolithic transition and a large contribution as supporting the demic diffusion model. However, Haak et al. (2010) and Brandt et al. (2013) suggest that there was a major demographic event after the early Neolithic, which would mean that this interpretation would be problematic. Furthermore, clines in genetic frequency could also arise from the first peopling of Europe or re-colonisation after the LGM, admixture between groups with allele frequencies which were initially different (Barbujani and Bertorelle, 2001), natural selection (Fix, 1996), range expansion or genetic drift (Pinhasi et al., 2012). Lazaridis et al. (2014) find that contemporary Europeans do in part derive from European farmers who were mainly from SW Asia, but there are also at least two other ancestral populations.

Studies using ancient DNA have suggested a regional difference in how farming was spread; with some evidence for cultural diffusion in Central Europe (Haak et al., 2005) and demic diffusion in the Mediterranean (Sampietro et al., 2007). Ancient DNA work has also shown a genetic affinity between modern SW Asian and early Neolithic samples in both Central Europe and in the Mediterranean (Brandt et al., 2013; Gamba et al., 2012; Haak et al., 2010), and also between modern southern Europeans and an early Neolithic Scandinavian farmer (Skoglund et al., 2012). This work suggests that pioneering farmers travelled from SW Asia to all over Europe, and Hofmanová et al. (2016) suggest that this dispersal would have been from the Aegean.

Ancient DNA studies have also shown a large genetic difference between hunter-gatherers and early Neolithic populations in Central Europe (Bramanti et al., 2009; Brandt et al., 2013; Haak et al., 2010, 2015) and Northern Europe (Skoglund et al., 2012), which again further supports an idea of early farmers as immigrants rather than local hunter-gatherers adopting a new culture. Taken together, recent ancient DNA studies favour the demic diffusion of farming into and across Europe by migrating farmers originated in western Anatolia, but that there was a later partial resurgence of hunter-gatherer ancestry as farmers and hunter-gatherers mixed in the middle and Late Neolithic.



(a)

(b)

(c)

Figure 1.6: (a) The spread of farming across Europe based on archaeological evidence (figures give the approximate earliest dates in years BC). Taken from Burger and Thomas (2011). (b) Different intensities of the first principal component of the gene frequencies from 38 independent alleles from ten loci. Taken from Menozzi et al. (1978). (c) The relative frequencies of 6 pools of Y-chromosome haplotypes which account for 95% of the samples (colours), the remaining 5% are grouped together and shown in white. Taken from Semino et al. (2000).

1.3 Understanding the Origins of Agriculture

Archaeological work can give us a good picture of where and when agriculture first developed, and genetics can help us understand how it spread, but fully understanding how and why it began is challenging. This requires us to not only consider archaeological and palaeoclimatic evidence, but also human behaviour.

In this section I will discuss how certain pressures and changes could have lead to the origins of agriculture both directly and indirectly. I will then introduce human behavioural ecology (HBE), and discuss how this can be used as a framework to understand the switch in subsistence strategy.

1.3.1 Climate Stress

The right climate conditions for agriculture are obviously necessary for its development, but the role that climate conditions are suggested to play varies from some authors implying that it is a direct cause, to others suggesting it is indirect and acted as a trigger for a series of events, including demographic pressure, leading to agriculture.

One of the first direct climate-based theories is that of the ‘Oasis hypothesis’ by Childe (1926). This is based on the idea that due to the Holocene’s warmer climate areas became arid and thus forced humans and animals to settle by lakes and rivers, and it was this close proximity with animals that could have prompted their domestication (Bar-Yosef, 1998). However since domestication actually started during a wet climate phase this theory is contested (Bellwood et al., 2005). Wright (1977) also argued that the climate change of the Holocene played a major part for the origin of agriculture. His hypothesis was that pre-adapted wild cereal grains immigrated into the Fertile Crescent from dry-summer Mediterranean climates, which spurred their selection for domestication.

Moore and Hillman’s (1992) excavation of the site of Abu Hureyra found changes in the archaeobotanical material coinciding with the Younger Dryas – the reduction of certain species and increasing abundance of others. From these results the authors suggested that the severe climate changes of the Younger Dryas acted as a catalyst for the development of agriculture in SW Asia, where these stresses forced people to start cultivating certain species. Alternatively, these archaeobotanical changes could also be because of the broadening of plant foods in the diet (Colledge and Conolly, 2010).

Although agriculture began at the beginning of the Holocene in SW Asia, this was not the case worldwide, and thus many direct-cause climate theories can be disregarded somewhat (Bellwood et al., 2005; Cohen, 1977). Perhaps more robust are the models which support the idea of climate change as the cause of subsistence experimentation and other lifestyle changes, eventually leading to agriculture.

McCorriston and Hole (1991) suggest that in the Southern Levant seasonal resource shortages due to the instability of the late Pleistocene meant that people developed storage. Storage encouraged sedentism, which in turn meant people depleted local resources quickly, and therefore the use of subsistence strategies which would lead to domestication became advantageous. However, another (perhaps more likely) solution to seasonal resource shortages could be increased mobility (see Section 1.4).

Whether climate change was a direct or an indirect cause of agriculture, the right climate conditions were a necessary backdrop. As Zeder and Smith (2009, p. 683) notes:

> (...) climate change alternatively helped push and pull societies along the pathway to domestication and agriculture, providing both opportunities and challenges that people across the broad arc of the Fertile Crescent responded to in a variety of ways, depending on their local cultural and environmental settings – forming a rich mosaic of alternative adaptive solutions.

More specifically, Richerson, Boyd and Bettinger (2001) argue that agriculture was both impossible during the Last Glacial, and compulsory in the Holocene. They hypothesise that due to the high-frequency of climate fluctuations, lower levels of atmospheric CO_2 and the fact that the cultural evolution of agricultural subsistence systems is a slow process, agricultural evolution could not have occurred in the Last Glacial. In the Holocene, however, they (and also Diamond, 2002) hypothesise that the increasingly stable climate allowed for plant-rich subsistence intensification and groups with the most efficient use of the land out-competed others, which in some cases would lead to the evolution of agriculture.

1.3.2 Demographic Stress

The effects of population pressure have also been suggested as a driver for the origins of agriculture. This idea generally supposes that a stress on the resource availability for a population promotes subsistence intensification, eventually leading to a change in the subsistence system (Cohen, 1977). The idea of population pressure has often been assumed to mean a high population density, but Cohen (2009) has also suggested that declining resources and political pressure could also be causes for population pressure, and relief from these could be sought in an expansion of food choices or to work harder, which could have been the precursors to agriculture.

Binford (1968) and Flannery (1969) proposed that due to the late Pleistocene rise in sea level, people living in some coastal areas would have a comfortable sedentary lifestyle based on a subsistence of migratory birds and fish. However, these areas would soon reach high population densities and people would then migrate into suboptimal habitats (e.g. the gravel desert parts of SW Asia) where the carrying capacity of the area would be reached most quickly.

Richerson, Boyd and Bettinger (2001) develop a model to show that the maximum carrying capacity should have been reached, worldwide, much earlier than 11,600 yBP, and thus argue that the population pressure argument does not explain why agriculture began. Furthermore, they assert that if agricultural innovation was a quick process the population pressure argument would mean that populations in the Pleistocene would be switching between agriculture and hunter-gathering regularly due to the variable climate creating subsistence crises repeatedly. Flannery (1973) also notes that a population pressure model based on population density does not hold globally as in Mesoamerica population densities were very low when agriculture first developed. Furthermore, Zeder and Smith (2009) note that the specific regions of the Fertile Crescent where initial domestication began have little evidence for population pressure.

1.3.3 Internal Changes and Social Forces

The hypotheses discussed so far are mostly based on external forces, but there are also some theories for how changes within and between people could have lead to the development of agriculture.

Rindos (1984) proposed an evolutionary model for the development of agriculture, based on the idea of a long period of mutualism between plants and humans starting with the chance domestication of wild plants. However, Redding (1988) suggests that this theory misses the point somewhat, and the selective pressures that maintained this mutualism still need to be identified.

Braidwood (1960) proposed the idea of ‘cultural readiness’, where agriculture developed due to human communities reaching high levels of cultural differentiation and specialisation. In this theory people were simply so in tune with their habitat that they started domesticating the plants and animals which they knew so well. Braidwood suggested that this cultural level was reached first in the Fertile Crescent, and later in Central America, southeastern Asia and China, and spread from these centres to the rest of the world by cultural diffusion. Richerson, Boyd and Bettinger (2001), however, suggest that Braidwood’s hypothesis has the wrong time scale, and agriculture should have developed much earlier if it was only reliant on cultural ‘settling in’.

In a similar type of argument, Cauvin (2000) suggests that the shift to agriculture was driven by a change in the way of thinking about nature – from feeling part of it, to feeling in control of it.

However, some of these hypotheses rely on an idea of early farmers being somehow more cognitively sophisticated than their predecessors, which is difficult to support and underestimates hunter-gatherers. The Jomon culture of Japan serves as a counter argument to these theories, since the Jomon were culturally complex, semi-sedentary, lived in large settlements and had storage, but did not have an independent transition to agriculture (Bleed and Matsui, 2010).

Bender (1978) called for social forces resulting from the demands of the evolution of social relations to be considered in explanations for the origins. For these explanations it may be predicted that agricultural development would correlate with the emergence of socio-economic complexity – which could be measured by the archaeological evidence of sedentism, hierarchies, storage, prestige items and exchange (Winterhalder and Kennett, 2006).

Social stresses, such as competition between individuals or groups, could promote farming as a way to create rewards, for example to support larger population size or strength (Bellwood et al., 2005). Hayden’s (1990) competitive feasting theory follows a similar argument, but in this case the reward is the ability to create surpluses. This theory is based on the idea that technological innovations – such as mass fishing and gathering, processing and storage technologies – during the Mesolithic made the production of resource surpluses possible. With surpluses comes the ability for people or groups to hold feasts, which could create debt, control, competition, rivalry and social inequality amongst populations (Hayden, 1996, 2009). Hence, there were socio-economic benefits to have enough surpluses to hold a successful feast and Hayden suggests that these created a continuously increasing demand on food production, which eventually would lead to agriculture. Furthermore, Hayden claims that the competitive feasting model can explain why the first domesticates are not as expected, e.g. chilli peppers and dogs instead of wheat and goats – they may have been prestige items. However, Winterhalder and Kennett (2006) argue that the competitive feasting theory does not explain why agriculture would emerge roughly simultaneously (unlike behavioural modernity Powell et al., 2009) in different regions, and is also at odds with the fact that in some parts of the world domestication occurred before the right conditions for surpluses to accumulate arose.

Zeder and Smith (2009) support Rindos's (1984) mutualism theory, but rather than a random mutation of behaviour leading to chance domestication, they prefer the concept of niche construction. In this, humans consciously tried to reach certain social and economic goals within particular environmental and social conditions, leading to a change in the subsistence system.

1.3.4 Human Behavioural Ecology

Human Behavioural Ecology (HBE) can be used to understand why foragers changed their behaviours (e.g. becoming sedentary, moving to suboptimal environments, or increasing the breadth of species foraged for) in response to some of the pressures noted in the preceding paragraphs. HBE frameworks use evolutionary theory to explain the process of behaviour change, rather than just explain the causes for it.

In much the same way as the changing frequencies of genes through natural selection, evolutionary theory can be used to understand behaviour change and diversity. By also bringing in elements from economics, such as game-theory and optimisation, behaviours can be understood in terms of their cost effectiveness or efficiency. In this sense, HBE is a framework in which to see behaviour change and diversity as an adaptation to ecological variables.

HBE was initially developed in the 1970s to understand how hunter-gatherers move around a region whilst foraging – a key outcomes of which was optimal foraging theory (OFT; Wilmsen, 1973). OFT states that the most efficient (usually in terms of energy) foraging pattern will be selected for, and in this context different human and nonhuman foraging behaviours have been studied. An important factor in this is the law of diminishing returns (e.g. because of resource depletion), and hence the foraging organism needs to decide the optimal time to leave a resource patch (described as the marginal value theorem; Charnov, 1976).

HBE based explanations for the switch to farming discuss the idea that economic efficiency can be used to understand the switch to agriculture – by calculating relative costs and benefits of foraging and farming.

The diet breadth model is a possible explanation in the HBE framework for the broad spectrum revolution (see Section 1.1.3). This predicts that if high ranking resources become limited (perhaps due to climate changes), it becomes more efficient to incorporate lower ranking resources into the diet rather than to continue to search for rare prey. Lower ranking resources may be more plentiful, but require more effort or culturally transmitted skills in harvesting and processing (e.g. seeds and tubers; Winterhalder and

Goland, 1993). This change leads to a broader diet where foragers have an overall lower energy cost to searching for food (Gremillion and Piperno, 2009). Additional to a broad diet being more efficient, some of the new foods that entered the diets may have also been more sustainable (e.g. some had high reproductive rates; Stiner, 2001). In terms of the transition to agriculture, the diet breadth model shows how certain foods (e.g. cereals) may have entered diets, and after some time of exploitation and management, become the first domesticates (Gremillion and Piperno, 2009).

1.3.5 Summary

The large time-lag between the beginning of the Holocene and early cultivation in some parts of the world mitigates against the direct-cause climate hypotheses for the origins of agriculture. There is some possible counter evidence for the demographic pressure argument (e.g. Mesoamerica), and also many hunter-gatherers exhibited complex social behaviour and technological knowledge well before agriculture began. Thus, there is no clear explanation for the origins of agriculture.

The climatic effects of the Pleistocene-Holocene transition clearly had effects on how people lived, whether this was by promoting more or less movement, changing the types and breadth of foods foraged, or perhaps storing more food as a risk aversion strategy. These changes would prompt even more transformations and perhaps exert more pressures (for example decreased mobility could lead to demographic pressure). Hunter-gatherers may then have had the ability (perhaps cognitively or via the introduction of a new suitable species for exploitation) and/or the pressure for a more reliable way of procuring resources, to start to cultivate. Hence, from a starting point of environmental changes people would have had to reassess the efficiency of how they lived, which could lead to an agricultural economy. The events along this path would have been different within and between different regions of the world.

1.4 Hunter-gatherer Mobility

Since becoming sedentary is inextricably linked with the origins of agriculture (as discussed in Section 1.1.3), in this section I will describe hunter-gatherer mobility and reasons for variation in it. Much of this discussion is within the HBE framework. I will give summaries of ethnographic data on hunter-gatherer mobility in Section 2.5.1.

One of the obvious reasons for hunter-gatherer mobility is the search for resources (Grove, 2009), or better ones (Anderies and Hegmon, 2011), and since foraging areas can quickly become depleted, hunter-gatherers are generally quite mobile. However, there are some ecologies (for example along coastlines) where resources are more abundant, predictable and less easily depleted, and in these hunter-gatherers can have reduced mobility (Hamilton et al., 2016; Kelly, 2013).

A classic model for hunter-gatherer residential mobility is Binford's (1982) 'complete radius leapfrog pattern'; this is shown in Figure 1.7. This model assumes bands need to move to a new base which is twice the distance of the foraging radius in order to not forage in an already depleted area. Additions to this simple model include the circumstances which affect how big the foraging radius is (and therefore how big the move distance is) (Grove, 2009).

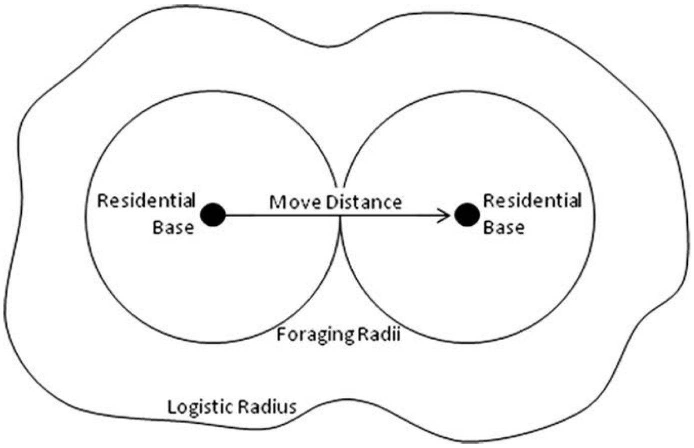


Figure 1.7: A diagram of Binford's 'complete radius leapfrog pattern'. Taken from Grove (2009) (fig. 1) interpretation of fig. 2 from Binford (1982).

1.4.1 Why Move?

It is generally accepted that foragers move because they have depleted, or considerably reduced, the resources in the foraging radius around their residential base. And it can be seen that high mobility is indeed correlated with a smaller population density, less food availability (from high primary biomass), less dependence on fish or a higher effective temperature (this will be illustrated using ethnographic data in Section 2.5.1 when I look at data from Kelly (2013)).

A decrease in mobility can be predicted in the optimal foraging theory (OFT) framework when there are high population sizes. Under these conditions food density can be relatively low due to depletion, and thus the net return of an individual moving to another low quality resource patch can be less than that of staying put (Bettinger and Baumhoff, 1982). On the other hand when population sizes are low Bettinger and Baumhoff (1982) predict foragers should move frequently amongst patches, which allows for other fitness enhancing behaviours such as mating. More movement also means that foragers may visit a larger breadth of site types, and thus increase dietary breadth. OFT can be useful when considering the reasons behind hunter-gatherer mobility decisions, but there are of course other factors influencing movement.

There are considerable costs to movement – for example energy, planning, predations and other risks, opportunity loss, and time (Hamilton et al., 2016) – so it might make sense that in particularly rich environments there is less benefit to mobility and thus it is reduced. However, there are also cultural reasons for movement, as Kelly (1992, p. 48) notes

> People also respond to religious, kinship, trade, artistic, and personal obligations (...) People move to gain access to firewood or raw materials for tools, or because insects have become intolerable (...) people seek spouses, allies, or shamans, or move in response to sorcery, death, and political forces (...) in order to visit friends, to see what is happening elsewhere, or to relieve boredom.

Similarly, mobility helps establish and maintain social networks which can reduce risks when resource availability is low (Whallon, 2006). There is also the argument that keeping mobile allows hunter-gatherers to maintain the knowledge of resources in a region and thus prepare for the possibility of unfavourable circumstances (Binford, 1983; Migliano et al., 2017).

Kelly (2013, p. 107) states that "sedentism is a product of local abundance in a context of regional scarcity". Therefore, for homogeneous environments depletion will always play a part, and movement (even if infrequent) always has some benefits. Kelly argues that the only reason not to move would be if there was nowhere for groups to move to, which could be the case for high regional population densities. For heterogeneous environments, on the other hand, movement has fewer benefits and sedentism may be more likely. Kelly also suggests that since the presence of sedentary groups in a region removes possible resource areas from mobile groups, this might create a domino effect of switching to sedentism.

Other explanations for mobile foragers becoming sedentary are given by Price and Brown's (1985) 'pull' and 'push' hypothesis – where resource abundance encouraged less mobility (pull), or resource scarcity led to more time harvesting and processing and therefore less time spent moving (push).

Thus for reduced mobility to occur the resources in the local environment will probably be abundant and reliable, but not necessarily high ranking.

In SW Asia and in China there were increases in population size and sedentism before agriculture. In contrast agriculture is thought to have begun before sedentism in the Neotropics where sites were seasonally occupied. Furthermore, sedentary foraging was not followed by an independent transition to farming in Japan (Bleed and Matsui, 2010) and the northwest coast of North America (Dow and Reed, 2015). There are also agriculturalists/horticulturalists who are mobile, for example the Rarámuri in northern Mexico (Hard and Merrill, 1992). And Kelly (1992) argues that there is evidence that reduced mobility and agriculture were not linked (or only in a minor way) in the Gulf Coast of Florida, the Levant, the American Midwest, and coastal/highland Peru.

1.5 Thesis Summary

In this chapter I have summarised how the transition to agriculture has had profound implications on how we live now, and that it is well studied archaeologically. I have also shown how genetics can help us understand how farming spread geographically. However, I have also discussed how, despite many theories, there is no global consensus on why and how agriculture began. I discussed how applying evolutionary theory in the form of human behavioural ecology (HBE) provides a useful framework for exploring why late Pleistocene forager groups changed their behaviours. I also examined why hunter-gatherer mobility can vary, and how a HBE framework can also be used to understand this variation.

Modelling can be used to test hypotheses and build theories about past events. Thus, to understand the origins of agriculture better – the goal of this thesis – in the next 6 chapters I implement and analyse several evolutionary models.

In Chapter 2 I explain how evolutionary theory can be applied to human behaviour, discuss game theory, agent-based modelling and how modelling can be used in theory building. I then review some of the existing mathematical models for the origins of agriculture and related concepts, and discuss the motivation for developing a new model. I also introduce some of the methodological contributions I have developed, including a statistical method for parameter analysis – fitting to idealised outcomes (FIO). I finally discuss and analyse the ethnographic, archaeological and climate data I have to inform my development of my model.

In Chapter 3 I present my work on replicating and analysing a mathematical model for the origins of agriculture and property rights by Bowles and Choi (2013). This work serves as an example of applying the FIO method and noting the extra insight it offers. I describe the model, the methodology of applying the FIO method, and the results found. The work for this chapter is published (Gallagher et al., 2015).

In Chapter 4 I describe an agent-based model I developed to study foragers and their mobility decisions in a region. This model considers the feedback between people and their environment, and includes the mutation of strategies, population growth and resource depletion processes. The analysis and results of running this model are discussed in Chapter 5.

An extension of this model is given in Chapter 6, along with the analysis and results found. These extensions allow agents in the model to forage or farm, and hence I can investigate the relationship between subsistence, mobility and population size. In both Chapters 5 and 6 I investigate the impact of environmental conditions, interactions within the model, temporal and spatial variation, and the order of events, amongst other things.

Finally, in Chapter 7 I give the conclusions of this thesis and discuss further work.

2

Modelling and Data

> *"There's no sense in being precise when you don't even know what you're talking about"*
>
> – John von Neumann

Summary

In the previous chapter I illustrated some of the many factors, interdependencies and discrepancies associated with the origins of agriculture. Because of these, producing a clear picture of the causes for and the processes involved in the transition is difficult. I also discussed how human behavioural ecology (HBE) can be a useful framework with which to understand the behaviour changes associated with the origins.

Models can help to sharpen intuitions, reveal unexpected behaviours and test hypotheses, and are especially valuable when trying to understand past events where real time experiments are not possible. Modelling is also a useful tool to fill in gaps when data is unavailable, which is often the case in archaeology. However, modelling is also reliant on data for informing assumptions and testing. Therefore when building a model it is important to understand the limits to the data you have available, and model accordingly.

I will begin this chapter by discussing how evolutionary theory can be applied to human behaviour in general. Concepts discussed in this section will be referred to later in this thesis. In Section 2.2 I will then discuss modelling both in general and as applied to social behaviour, giving particular emphasis to agent-based modelling and evolutionary game theory. In Section 2.3 I will review some of the existing models concerned with the transition to agriculture and associated processes.

I will then discuss in Section 2.4 some of the methods I developed in this thesis, including a parameter sensitivity analysis (fitting to idealised outcomes, FIO) that I go on to apply to the models in Chapters 3 and 6. Next, in Section 2.5 I will discuss and analyse the ethnographic, archaeological and climate data I have available, which I go on to use in the development of my own models in Chapters 5 and 6. I will conclude this chapter in Section 2.6.

2.1 Evolutionary Theory and Human Behaviour

In the 1960s Darwin's theory of evolution by natural selection started to become more frequently applied to study human behaviour; for example the work on kin and group selection and reciprocal altruism (Hamilton, 1964a,b; Maynard Smith, 1964; Price et al., 1970; Trivers, 1971). Using genetic evolution to understand the social behaviour (sociobiology) of animals, for example pack hunting and mating patterns, was first popularised in 1975 when E.O. Wilson published *Sociobiology: The New Synthesis.* This book sparked much controversy since in its extreme (genetic determinism) sociobiology ignores the cultural explanations for behaviour. Thus its application to human behaviour has the potential to fuel racist and other prejudiced viewpoints.

Memetics on the other hand, is almost the opposite. In memetics human behaviour is studied in terms of cultural units (referred to by Dawkins (1976) as *memes*) which may spread in a population without human choice. Hence in the nature-nurture debate on human behaviour, it could be thought that sociobiology can help to understand the nature elements and memetics can be used for the nurture elements. However, human behaviour is much less discretised than this and, quoting Laland and Brown (2011, p. 12), "a complete understand of human behaviour will result only from us studying human beings as animals developing in a rich social environment and immersed in complex cultural traditions".

In the wake of human sociobiology shortcomings, the fields of human behavioural ecology, evolutionary psychology, cultural evolution and gene-culture coevolution, all attempt to integrate cultural elements into the evolutionary theory of human behaviour. For an extensive discussion of these see Laland and Brown (2011).

Human behavioural ecology (HBE) applies evolutionary theory to human behaviour whilst considering the environmental context – this was discussed in more detail in Section 1.3.4. HBE is a framework to think about human behaviour with, and hypotheses developed through HBE can be tested by looking at how humans really behave. HBE however assumes that humans have the ability (whether consciously or not) to optimise their behaviour, which in many circumstances may not hold. It also assumes that the behaviour observed is already optimal, rather than still actively changing to its optimum (Boyd et al., 2011). HBE also often ignores constraints on adaptation, such as developmental constraints and trade-offs.

Rather than thinking of the behaviour as the evolving entity (as HBE does), evolutionary psychologists look at the psychology which leads to behavioural decisions as the evolving entity (Symons, 1989). Evolutionary psychologists suggest there is a lag between our current environment and the environment we were psychologically adapted for (which is taken as the Pleistocene), and as such evolutionary psychology can be used to look at the adaptive problems of our ancestors (Cosmides and Tooby, 1987). However, the Pleistocene may have been too unstable to allow for very specific cognitive adaptations (Brown and Richerson, 2014), so evolutionary psychology alone may not account for the behavioural flexibility necessary for the cultural complexity humans have (Boyd et al., 2011).

By borrowing methods and concepts from biological evolution, and as in memetics thinking of culture in the same way as genes, cultural evolution can be used to understand how human behaviour changes at the individual and population level. Cultural evolution also uses mathematical modelling, rather than storytelling (a common criticism of memetics, HBE and evolutionary psychology; Laland and Brown, 2011) to understand human behaviour. Cultural evolution looks at how behaviour variants can change in frequency; this includes the ability of behaviours to be transmitted (analogous to inheritance), copied (analogous to horizontal gene transfer), changed via innovation (analogous to mutation), combined in new ways (analogous to genetic recombination), and changed randomly (analogous to genetic drift). Because of differential fitness of behaviours in a population, some behaviours may become selected for and increase in frequency. In cultural evolution models, how the behaviours are copied is an important consideration (Boyd et al., 2011). A criticism of cultural evolutionary approaches is whether or not human behaviour should be modelled in the same way as biological evolution, or whether there are other mechanisms at work.

Cultural and genetic evolution can interact – culturally selected behaviours can affect the gene pool, and natural selection can affect the frequencies of cultural traits. In gene-culture coevolution theory human behaviour is studied in terms of these interactions and feedback. Human behaviour can also shape the environment in which we live, which can in turn affect selective pressures – this is referred to as niche construction. For example, as dairying culture expanded after the domestication of animals so later did the ability to digest lactose in adult life (a trait determined genetically), which in some environments would have been an huge advantage over those who could not (Gerbault et al., 2011; Itan et al., 2009). If a demic diffusion model of the spread of farming is true (as discussed in Section 1.2), then the frequency of the ability to digest lactose in modern day people should be correlated with the spread of farming.

Thus the application of evolutionary theory to understanding human behaviour can be done in different ways. I will discuss modelling and game theory in more detail in the next section as these are important in the application of HBE frameworks and cultural evolution.

2.2 Modelling

There are many types of mathematical and computational model. Very broadly models can be *stochastic* where there are random elements to the model or *deterministic* where there is no random elements. Having random elements in the model means that each time the model is evaluated the results will be different even if the same parameters are used. Models can also be either *mechanistic* where the system's behaviour is modelled with an understanding of the workings of its individual parts, or *empirical* where extensive observed data and measurements are used to model the system. Models can also be *dynamic*, where model observations change with time, or *static*, which are at equilibrium; some model *discrete* states, and others look at *continuous* changes; *explicit* models are when you know the input parameters and are calculating the outcomes, and *implicit* models where you know the outcomes of the modelled process and are finding the inputs.

Depending on the information you have about what you are modelling, and the type of questions you want to ask, different model frameworks will be appropriate. These frameworks include statistical models, equation-based models, system dynamics, and simulation approaches such as discrete event simulation and agent-based models.

In this section I will discuss frameworks which are useful in modelling social behaviour. These include evolutionary game theory, evolutionary algorithms and agent-based modelling. I will also discuss some general concerns around parameter choice and analysis, and how modelling fits within the scientific method.

2.2.1 Evolutionary Game Theory

A framework in which to model social behaviour can be in the context of games. Game theory was conceived in 1928 by John von Neumann (Neumann, 1928). It generally involves a single or multiple round contest in which all players have a choice of strategies to play. According to certain rules, each combination of possible players' strategies in a contest have different payoffs. It is of interest to find the scenarios in which certain strategies maximise payoffs and is often used to understand economic, political, social and biological strategic behaviour.

The popular example of the use of game theory is the Prisoner's dilemma. This has been used to study the cooperation/defection decisions in a game between two players. Although easily adapted to many different scenarios, the original set-up to this game looks at a situation in which two people are arrested on little evidence, isolated from one another and then given the opportunity to betray the other prisoner. There are three

Table 2.1: Payoff for player 1 when interacting with player 2 in the Prisoners Dilemma game

	Player 2 – Silent	Player 2 – Betrays
Player 1 – Silent	1 year	3 years
Player 1 – Betrays	Goes free	2 years

options that can occur depending on whether the prisoners betray each other (defect) or remain silent (cooperate):

1. Both prisoners betray each other – they both receive a 2 year sentence
2. One prisoner betrays the other, and one remains silent – the betrayed prisoner receives a 3 year sentence, and the other goes free
3. Both prisoners remain silent – they both receive a 1 year sentence

These payoff combinations are summarised in Table 2.1. Therefore, at an individual level defection can mean going free, but overall mutual cooperation is better than mutual defection, and herein lies the dilemma. The prisoner's dilemma can be adapted in many ways; it can be discretely or continuously iterative, include a memory for past interactions (peace war game), or include stochastic and spatial elements.

In part developed by the evolutionary biologist John Maynard Smith (Maynard Smith, 1972; Maynard Smith and Price, 1973) evolutionary game theory (EGT) looks at the strategies of players as evolving entities. Players in evolutionary games can replicate and pass on their strategies. A player's payoff is thought of as its fitness, and fitter players are more likely to replicate. Therefore, as in natural selection, fitness maximising strategies will persist in the population.

Whilst in classic game theory successful strategies are the ones that maximise individual payoff, in evolutionary games the most successful strategies are the ones which can persist in the presence of other competing strategies. Hence in evolutionary games the frequencies of the strategies in the population affect their success.

EGT was developed originally to study intraspecific conflicts between two individuals which have different behaviour types. Maynard Smith (1973) studied this using a game where there were five different possible behaviour types – dove (although in Maynard Smith and Price (1973) this type is described as 'mouse'), hawk, bully, retaliator, prober-retaliator. In the game with only two of these behaviour types (the hawk-dove game) there is a contest between two players (which are either a hawk or a dove) over a

Table 2.2: Payoff for player 1 when interacting with player 2 in the Hawk-Dove game

	Player 2 – Hawk	Player 2 – Dove
Player 1 – Hawk	V/2 – C/2	V
Player 1 – Dove	0	V/2

resource of value V and if a fight ensues the loser pays a cost, C. The outcomes for each type of pair are:

1. Hawk meets Dove – Hawk takes all the resource (V), Dove receives nothing (0)
2. Hawk meets Hawk – a fight occurs, each win the resource with a probability of 1/2, the loser pays the cost
3. Dove meets Dove – both share the resource

The payoff combinations are summarised in Table 2.2. The game also includes the proportions of hawks and doves in the population, and hence the payoffs are multiplied by the probabilities of encountering a hawk or a dove. The game is also generational, so at the end of every round of contests (games) there can be replication and death of contestants, and hence the next generation can have different proportions of strategies, which can in turn affect how successful certain strategies are. The strategy which will still remain dominant even with invasion from other strategies (if initially rare) is referred to as the evolutionary stable strategy.

An additional behaviour type to the hawk-dove game is the 'bourgeois' (Maynard Smith, 1986). This behaviour type acts differently depending on who is the owner of the resource being fought over and who is the intruder. A bourgeois plays hawk if it is the owner of the resource, and plays dove if it is the intruder. In this way, a bourgeois behaviour respects ownership.

2.2.2 Evolutionary Algorithms

Cultural evolutionary models of social behaviour can be made in which individuals interact (socially and with their environment, perhaps according to a game) and evolve. These models fit into the broader category of evolutionary algorithm. Evolutionary algorithms, inspired by natural selection, consist of a population of individuals which have some fitness measure. The most fit individuals are more likely to reproduce, where mutation and recombination can occur during reproduction, and individuals with the lowest fitnesses can die.

In these models it is possible that certain strategies will be selected for and unpredicted and possibly complex behaviour of the system can emerge without having been specifically programmed into the model. In this way we can study which circumstance give rise to the 'natural' evolution of certain strategies/behaviours in various environments. Agent-based modelling can be a good model option since these models are focussed on individuals who 'live' according to rules.

2.2.3 Agent-Based Models

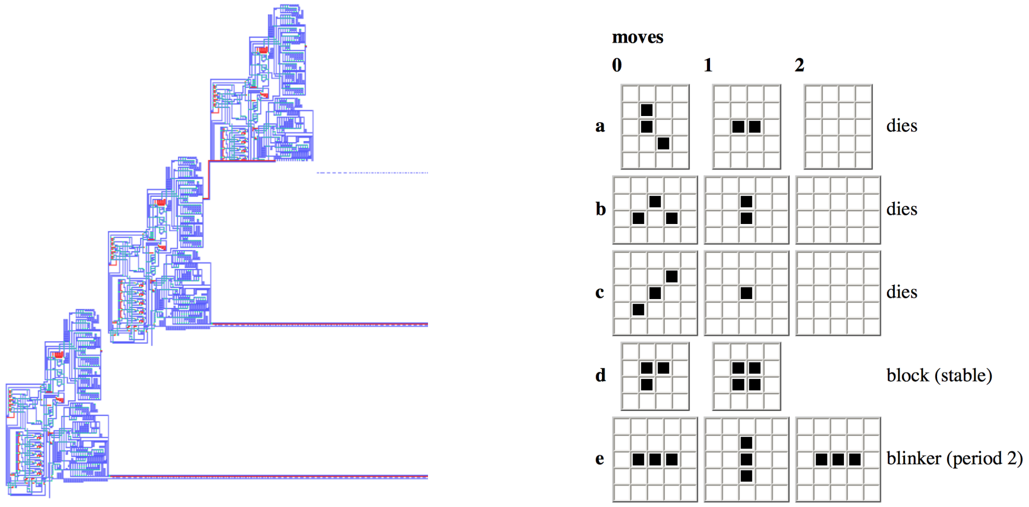
Agent-based models (ABMs) are a type of simulation model where the behaviour of a system is determined by the activities of autonomous individuals (or agents). Agents can interact, move, adapt and learn according to predefined, but often simple, rules. Through this approach complex behaviour of the system can emerge.

Macal and North (2010, p. 152) state that the three main elements in a typical agent-based model are:

1. "A set of agents, their attributes and behaviours.
2. A set of agent relationships and methods of interaction: An underlying topology of connectedness defines how and with whom agents interact.
3. The agents' environment: Agents interact with their environment in addition to other agents."

Agent-based models emerged from work on cellular automata (CA), the first of which was created by John von Neumann and Stanislaw Ulam in the 1940s. Their idea was to try to build a self-replicating machine (a machine that can autonomously reproduce itself) and the solution was a complicated set of rules on a grid (Figure 2.1a). In 1970 John Conway simplified this idea in his Game of Life (1970). This game involves a grid of cells in which every cell interacts with its eight neighbouring cells according to four basic rules which decide whether the cell will live or die, see Figure 2.1b. These basic rules create many different emergent and complex patterns including one which copies itself in the process of destroying itself.

In the 1970s one of the first agent-based models was developed. This model was developed by Schelling and was used to study segregation (Schelling, 1971). In this model agents make decisions and interact with one another in an environment – contrasting with CA models where it is only the environment that is considered. In Schelling's model two types of agents can move around a grid, where an agent will move its location if



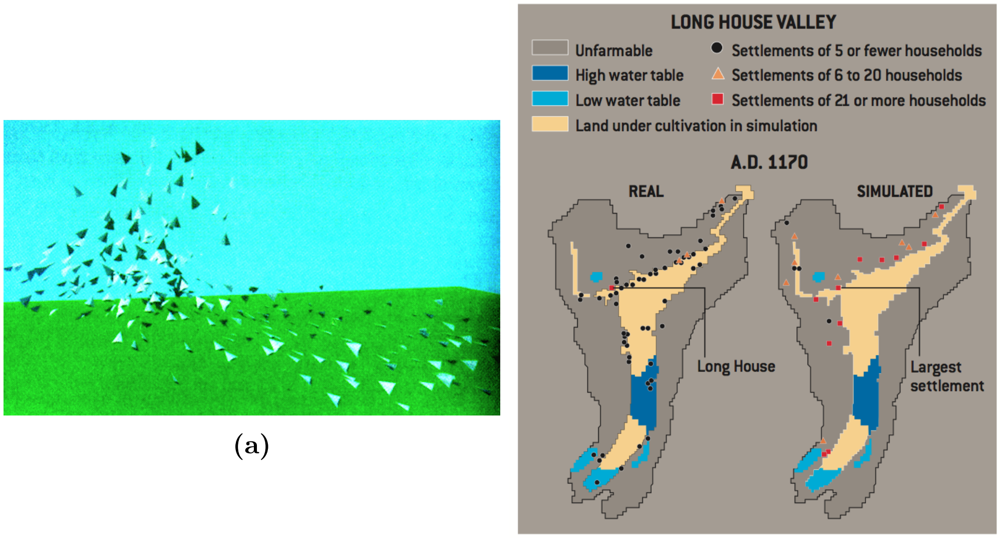
(a) **(b)**

Figure 2.1: (a) A version of von Neumann's design for a self-replicating machine (Szangolies, 2015). (b) Examples of 5 different configurations over 3 moves in Conway's Game of Life (Gardner, 1970).

it has a majority of immediate neighbours of the other agent type. After a number of these moves the emergence of segregation of the two agent types can be seen.

After these initial developments and increasingly powerful computational power, agent-based models have become a popular tool in ecology, the social sciences, the life sciences and economics. Research using ABMs has included land-use (Brown et al., 2005), the flocking behaviour of birds (Reynolds (1987), see Figure 2.2a), predator-prey relationships between killer whales and other marine mammals (Mock and Testa, 2007), bumble bee behaviour (Hogeweg and Hesper, 1983), how culture changes and spreads (Axelrod, 1997a), the evolution of cooperation (Axelrod, 1997b), sharing information (Čače and Bryson, 2007), crowd behaviour during emergency evacuation (Pan et al., 2007), the adaptive immune system (Folcik et al., 2007), the spread of cancer (Preziosi, 2003), agricultural economics (Berger, 2001), and the simulation of whole artificial societies in the Sugarscape model of Epstein and Axtell (1996).

In archaeology, ABMs have been used to study the societal collapse of the Anasazi (Dean et al., 2000), and, for the Puebloan people who came afterwards, changes in their settlement types (Kohler et al., 2000), their disappearance (Kohler et al. (2005), see Figure 2.2b), and their food-sharing networks (Crabtree, 2015). Amongst many other things, ABMs have also been used to study social dynamics and structure (Chliaoutakis and Chalkiadakis, 2016), settlement patterns (Crema, 2014), patterning in surface ar-



(a)

(b)

Figure 2.2: (a) Simulating flocking behaviour in the Boids program (Reynolds, 1987). (b) Comparing real and simulated data from a model of Puebloen settlements (Kohler et al., 2005).

chaeological features (Davies et al., 2016), battlefield archaeological sites (Campillo et al., 2012), dependencies between population dynamics and Holocene monsoon precipitation patterns (Balbo et al., 2014), the Mayan social-ecological system (Heckbert, 2013), Roman Empire ceramic tableware trade (Brughmans and Poblome, 2016), and the cultural transmission of Great Basin projectile point technology (Mesoudi and O'Brien, 2008).

When agents interact with one another they may do so according to a game, and the strategies the agents have may be evolvable. Thus agent-based modelling, game theory and cultural evolution can fit well together when studying behavioural change. Furthermore, *how* and *why* behaviours change – Tinbergen's (1963) 'proximate' and 'ultimate' – can be studied by modelling at such an individual level.

2.2.4 Building and Validating Models

Building a model involves knowledge and assumptions about the system being modelled. Models are abstractions of reality, and therefore they do not have to contain every single factor to do with the system. Because of this, decisions on which important components to include in the model, and those which do not need to be included, need to be made. These decisions can be based on which dynamics you are particularly interested in, which aspects of the system you have information about (based on data), and subjective decisions about which factors are important.

Depending on the type of model, input parameter values can be found empirically, estimated, or (in the case of implicit models) predicted based on known outcomes of the system.

After building a model and running it, the model needs to be evaluated to check that it is providing a realistic estimate of the system – this is model validation. This can be done by checking that some aspects of the model fit to observed data. It is important that the same data is not used to both inform the design of the model and the test the fit of the model. Sensitivity analysis should also be used to investigate how input parameters affect the outcomes of the model. If there is uncertainty in the value for the input parameters then this analysis will give some idea of the degree to which this impacts the results from the model.

A commonly used type of parameter sensitivity analysis is investigating the effect of varying one parameter whilst keeping all the others at their default values (I will refer to this type of parameter sensitivity analysis as 'fix-all-but-one'). In Section 2.4.1 I will illustrate the merits and problems with this approach.

2.2.5 Modelling and the Scientific Method

The scientific method is a process of "systematic observation and experimentation, inductive and deductive reasoning, and the formation and testing of hypotheses and theories" (Andersen and Hepburn, 2016). In this way hypotheses can be continuously improved by refinement or rejection.

A model is a scientific theory about how the real-life system behaves, and hypothesis testing is equivalent to model validation (Bryson et al., 2007). Hence, every time we validate a model we can learn something new about how the real-life system might work, and then refine hypotheses about this system accordingly. Thus, in the next version of modelling a particular system we may have even more robust ideas about parameter values or relationships within the model.

In terms of understanding the past, the modelling process helps us to make predictions about what may or may not have happened – something which may not be possible by solely looking at the archaeological record.

2.3 Models for the Origins of Agriculture

In this section I will discuss some of the existing models which can be used to understand some of the key processes involved in the transition to agriculture. These models are reviewed since they both provided me with inspiration for the development of my own model and also illustrate the contribution modelling can make in understanding the transition to agriculture. This is not an exhaustive review of the models associated with the transition to farming, but rather the ones I felt were most relevant and interesting in my search of the literature.

Since changes in mobility are associated with the transition to farming, but could have occurred before the transition, first I will look at some models which investigate mobility out of the context of agriculture. The models by Anderies and Hegmon (2011), Freeman and Anderies (2012) and Dow and Reed (2015) all consider the movement decisions of individuals in an environment with variation in resource quality. The first two of these look at how the resource qualities can change directly because of population density, and the last, due to weather. Dow and Reed (2015) also include the effect of population growth and technological knowledge. Additionally, the model presented by Hamilton et al. (2016) considers mobility decisions in different ecosystems in the context of metabolic rates.

I then consider the existing models concerned specifically with the switch to agriculture. The majority of these models test hypotheses (including some of those mentioned in Section 1.3) for the transition to agriculture – including the effects of mobility and population pressure (Locay, 1989); environmental change and technological knowledge (Wirtz and Lemmen, 2003); technological knowledge and cooperation (Marceau and Myers, 2006); technological knowledge and population pressure (Baker, 2008); climate change and population pressure (Dow et al., 2009); and technological knowledge and climate change (Dow and Reed, 2011). More broadly the model by Freeman, Peeples and Anderies (2015) investigates the stable strategies for farming when domestication has occurred. I will finally briefly mention the model by Bowles and Choi (2013) which looks at the relationship between property rights, climate change and the transition to agriculture, this model will be described in much more detail in Chapter 3.

2.3.1 Forager Population Size and Mobility

Anderies and Hegmon (2011)

The model presented by Anderies and Hegmon (2011) was motivated by the Mimbres archaeological region in southwest New Mexico. This region had two main areas, one which was richer (more resources and a higher regeneration rate) but was more degraded, and one which was less rich and less degraded. The authors modelled a landscape with two areas with variation in their resource qualities to try to understand the relationship between migration and spatial variation in resource quality.

Their model has 14 parameters, including ones to do with resource regeneration rate, harvestability, cultural attractors and migration. They model people migrating between the two areas and harvesting a density-dependent renewable resource, and also model the case where there is no migration. Their model shows that differences in regeneration rates and harvestability can cause the situation observed in the Mimbres region; where at equilibrium the area with slower regeneration is less degraded than the area with a higher regeneration rate. Migration reduces welfare losses for the population overall, but has little impact on the heterogeneity of degradation.

Freeman and Anderies (2012)

Freeman and Anderies (2012) built a model to look at the dynamics between foraging decisions, resources and social relationships.

Their model is built on ideas from two previous static human population-resource models: the traveler-processor model by Bettinger and Baumhoff (1982) and the packing model by Binford (2001). The former assumes that when there are low forager population densities foragers should maximise their energy return by minimising the time spent in one patch and frequently move between patches. In contrast, when there are high forager population densities foragers should maximise their time harvesting from one patch. The latter model assumes that groups of hunter-gatherers primarily exploit their landscape by moving between its different foraging locations. However, once the landscape is 'packed' – when all the foraging locations are occupied by a group – groups will then fight or cooperate with one another to use the resources in each other's territories.

The mathematical model by Freeman and Anderies (2012) includes 12 parameters and the two dynamic variables: resource abundance, $x(t)$, at time t and foraging effort, $e(t)$. Foraging effort is based on the harvest and consumption time of foragers within a habitat, and is measured in work hours per day. $x(t)$ is measured as biomass per unit area. Resource abundance changes according to

$$\frac{dx}{dt} = G(x) - H(x, e), \tag{2.1}$$

where $G(x)$ is resource growth and $H(x, e)$ is resource depletion by harvesting. $G(x)$ follows the logistic growth equation, $G(x) = rx(1 - \frac{x}{k})$, where r is the maximum growth rate of the resource and k is the carrying capacity within a habitat. $H(x, e) = ph(x, e)$, where p is the population density (number of groups/unit area) and $h(x, e)$ is the harvest for one forager group.

Several different resource patches make up a foraging habitat, and resources cannot move between habitats (hence they are seen as plant resources). Forager groups move from habitat to habitat, evaluate whether or not to start to forage in that habitat, and if so, then determine when to stop foraging there. Private ownership of resources by foragers is not considered in this model, hence all resources are open-access. Furthermore, the time spent foraging takes away time from other activities such as the maintenance of social relationships, and hence foragers want to minimise their time foraging.

The model was analysed using bifurcation and stability analysis using different parameter values. It was found that if a resource base's growth rate decreases or the density of foragers increases in a particular habitat, then resource harvesting by the foraging group in this habitat will intensify. However, Freeman and Anderies found that this adaptation can lead to a vulnerable system and foragers face a risk. It was suggested that to increase the system's stability foragers may start to enforce ownership rules, become hyperaggressive and expand territory, decrease fertility or increase mortality, and/or invest labour to increase the habitat's productivity, perhaps by cultivating domesticated plants.

Dow and Reed (2015)

The model developed by Dow and Reed (2015) involves climate change, population growth and technological knowledge, and aims to investigate the switch from mobile to sedentary foraging.

Dow and Reed (2015) model a region divided into many production sites, where each site can be occupied by several agents. Production sites can have abundant or scarce food resources, and these can change randomly both spatially and temporally. Agents have one unit of time for labour, and this can be spent on two food collection methods – hunting (which is a mobile activity) and gathering (which is involves stationary methods). Food output at a site is

$$Y = \theta[f(L_f) + kg(L_g)] \tag{2.2}$$

where L_f and L_g are the labour inputs for hunting and gathering of all the agents at this site respectively. f and g are hunting and gathering production functions respectively, k is the productivity of gathering. θ is the weather at this site. There are no costs to movement between sites.

Dow and Reed (2015) find that when the region's weather is generally bad and has a high variance, hunting only is used and sites are abandoned every time the local weather at the site changes from good to bad. When the region's weather is better and has less variance they find that agents can stay at the same site even if the local weather changes from good to bad. They propose three reasons for this, one is that if there is less variation in productivity from good to bad sites, agents are more likely to stay at bad sites. Another reason they give is that better weather can lead to population growth and therefore sedentism. Their final reason is that population growth promoted by better weather can lead to technological innovation, which in turn creates sedentism. They explain that the final reason is non-reversible, so even if the climate then deteriorates sedentism can still persist.

Hamilton et al. (2016)

Hamilton et al. (2016) look at the predictability of hunter-gatherer residential mobility. Since mobility is driven by the need for energy, they use metabolic rates to predict the scale of mobility and the respiration of the entire ecosystem (as a function of temperature and precipitation) to predict variation in mobility across different ecosystems.

A territory of size A is divided into the home ranges, H_0, of the N individuals of size M living there. A home range is the area used by an individual to meet their metabolic needs (B) given the energy availability, R, of the local environment, and therefore $H_0 = B/R$.

Using data from Binford (2001) and Hein et al. (2012) Hamilton and colleagues (2016) find the average relationship between average distance per move and area per individual, temperature and also precipitation.

They conclude that their model shows an exponential increase in average move distance with decreasing temperature and precipitation. Since biodiversity increases with temperature, they suggest their results show mobility decreases with increases in biodiversity. They also note that the average distance per move is only minorly influenced by population size, and so they predict any population density factors affecting mobility would be because of limits to the size of the area, rather than the number of people. Thus they predict switches to sedentism in hunter-gatherers would be primarily caused by changes to the subsistence ecology.

2.3.2 Models for the Switch to Agriculture

Locay (1989)

An early model for the switch to agriculture was one looking at the effect of sedentism and population pressure by Locay (1989).

Locay's model includes families (two adults and children) living in a uniform and natural environment, and producing food for themselves. Agents live two generations, one as children and one as adults. At the end of childhood, agents can marry other adults and form new families. The number of children that survive until adulthood is proportional to the amount of food the family has. Furthermore, families have varying degrees of nomadism, and the amount of food required for a child to survive to adulthood increases with the degree of nomadism in the family.

Families can get food by either hunting and gathering, or by agriculture (or both). Two assumptions are made at this point, one is that hunting and gathering is more "intensive in land relative to labor" than agriculture; and the other is that high degrees of nomadism are detrimental to farming output. Thus Locay's output of hunter-gathering, X_H, and of agriculture, X_A, for a family are taken as

$$X_H = \theta_H g(\tau_H, a_H), \text{ and } X_A = \theta_A h(N) f(\tau_A, a_A), \tag{2.3}$$

where τ_i and a_i are the amount of labour/time and land the family has available for hunter-gathering ($i = H$) or for agriculture ($i = A$); g and f are functions increasing with τ_i and a_i; θ_H and θ_A are how productive the activity is; and h is a function decreasing with N, the degree of nomadism. Locay also assumes that the total time available for subsistence activities, $\tau(N, a)$ (where $\tau_H + \tau_A \leq \tau(N, a)$), increases with the amount of nomadism (based on the idea that a sedentary family would need to frequently waste time walking to their foraging or farming site), but at a decreasing rate (i.e. $\tau' > 0$, but $\tau'' < 0$).

Locay finds that a household with much more labour available than land will find hunter-gathering unattractive; if there is little labour available relative to land, hunting and gathering will be attractive; and if the labour available and land are closer to being equal then a family will engage in both subsistence activities. Furthermore, Locay shows that the relative gains of agriculture in comparison to hunting and gathering are increased with sedentism.

Locay also tests the hypothesis of population pressure on the switch to agriculture. By allowing families to have an increasing amount of land available (i.e. there is no set constraint) until all the land in the region becomes utilised (and then there will be a land constraint) Locay creates population pressure within the model. He finds that a population pressure increase lowers each family's available land, which both increases the attractiveness of agriculture relative to hunter-gathering and lowers the advantage of nomadism. Thus a population pressure increase could cause a switch to agriculture, both directly and indirectly via a switch to sedentism (which would increase the advantage of agriculture).

Wirtz and Lemmen (2003)

A deterministic model by Wirtz and Lemmen (2003) looked at the dynamics between human changes (culture, economy and migration) and environmental changes on a global scale. Their goal was to test if these human changes are adaptations to their environment.

The model consists of four variables, the ratio of established agricultural economies to non-agricultural, population density, the farming effort ratio, and technology efficiency index. Data on the regional distribution of different vegetation classes (e.g. grassland, tundra, hot desert) at 5000 yBP is used in the model. The net primary productivity (NPP) for each of these classes is also found as a measure of their temperature limitation index (where warmer climates have values close to 0, and colder climates have values close to 1, representing the constraint of cold temperatures on vegetative growth). They split the world into 197 regions, and categorise these regions as belonging to one of the vegetation classes.

The model is implemented with evolution equations explaining how each of the variables change with time in each of the world regions. Findings suggest that the transition to agriculture would have occurred without climate fluctuation, albeit not as early. Wirtz and Lemmen also infer from their model that a slow process of technological innovation and competition was a driving force for the transition to agriculture, rather than population pressure.

Marceau and Myers (2006)

The effect of technological knowledge and cooperation on the switch to agriculture are studied in a model by Marceau and Myers (2006). Individuals in their model each have a time which they use for leisure, food production, and security effort. Individuals can form cooperative bands, which are either comprised of all foragers or all farmers, and within a band all work (labour and security) and food is shared equally.

For farmers, the only gain in forming a band is to share security costs. Farming output is given as ϕf, where ϕ is the amount of agricultural technological knowledge, and f is a function of the time spent farming and the amount of land farmed by an individual. The foraging stock available for foraging bands changes according to the logistic growth equation – and it is assumed that the amount of land used in farming reduces the carrying capacity of the foraging stock. The amount of foraged food harvested is a function of total band effort, amount of stock, and the degree of foraging technology.

They start their model with a solely foraging economy, and thus assume that initially there is no agricultural technological knowledge (i.e. $\phi = 0$). When considering a population of only foragers and low levels of technology, Marceau and Myers find that the best strategy for all individuals is to form a single cooperative band, which helps avoid over-exploitation. However, as technology (both of foraging and farming) increases this single band breaks up into many bands, causing an increase in work and over-exploitation of the environment, which eventually can lead to a switch to agriculture. Thus, they show that technological progression could have damaged the integrity of cooperative bands, and thus lead to the transition.

Baker (2008)

A model by Baker (2008) looks at the effects of technological capability and population density on the transition to agriculture. The model assumes these are "symbiotically related", and that agriculture requires more technological knowledge then hunting and gathering.

Baker's model includes n individuals allocating their time to hunting and gathering (τ_H) or to farming (τ_F) on an amount of land (Z), where $\tau_H + \tau_F = 1$. Land and labour is needed for agriculture, and the land not used in agriculture is used by agents for hunting and gathering. The amount of land needed for agriculture by one agent, z, is proportional to the amount of time spent on agriculture, thus $z = \psi\tau_F$. However, if land becomes scarce due to lots of agriculture (i.e. if $Z < \psi n \bar{\tau}_F$), then it will be shared equally amongst the agents. Agents can also have children, the number of which is determined by the amount of food the agent produces, hence the population dynamics of their model are determined by the production economy of the population. Technological capability is included into the model in the function for hunter-gatherer and agricultural productivities, along with population density, resource base availability and the amount of time engaged in agriculture.

Results showed that among agricultural societies, larger amounts of technological sophistication result in higher population densities, and vice versa. However, for hunter-gatherer societies population density is unaltered by technology level, and 'technological spillovers' from centers of civilization are important for the transition to agriculture.

Dow et al. (2009)

Dow et al. (2009) argue that the transition to agriculture and the associated population changes were the result of climate changes. In particular, the Younger Dryas's climate reversal effects on local site heterogeneity and the ability for migration between these sites, is seen as the key force. They create an analytic model with region-specific climate variation (which is based on the average temperature and precipitation), and within-region differences in site 'quality', which is fixed for each location, to test this idea.

A geographical region in their model contains many production sites where foraging and cultivation can take place. People move in between these sites freely, with no distinction between nomadic or sedentary people. The productivity of foraging and farming are functions of climate, site quality, and foraging or cultivation labour respectively. In each period of their model, adults decide (based on the climate and site qualities) whether to move site or not. Next, labour is split between foraging and farming at each site food is obtained and the products of foraging or farming are all shared equally between this site's population. Finally, the adults are replaced by their offspring, where the number of children for each adult increases with the overall productivity of the site.

It was found that the population density at high quality sites increased, and in the short-run cultivation became more favourable at these sites. Focusing on southwest Asia, their model predicts population growth between 15-13,000 yBP, and then the climate shock of the Younger Dryas caused people to move to 'good' sites where local populations increased, which made cultivation more attractive than hunting and gathering, and thus the transition to agriculture began.

Dow and Reed (2011)

Dow and Reed (2011) model the evolution of food production technological knowledge, and how climate shocks can effect this. Technological knowledge is made up of techniques for acquiring, processing and storing different food resources. The amount of food produced from resource r is taken as $a_r g_r(k_r) f_r(n_r)$. Where the resource is in abundance a_r, is harvested with technique k_r (which is comprised on many skills) and labour n_r. Adults will know a subset of the full technological knowledge set, and some of this subset can be passed on (with some mutation) to their offspring's knowledge.

Dow and Reed ask "what environmental conditions are most conducive to technical progress?" and find that climate shocks (such as the Younger Dryas) induced technological experimentation. The authors hypothesise that this innovation could then have led to agriculture.

Freeman et al. (2015)

The human behavioural ecology framework model proposed by Freeman, Peeples and Anderies (2015) looks at the relationship between foraging, farming and resource productivity; their model links foraging theory and niche construction. They ask in what circumstances do people become farmers – or not – once domesticated plants have become available.

Their model involves the reproduction and growth of a forest, and the amount of time households spend foraging and/or farming. The households forage for the seeds produced by trees and/or farm a domesticated plant, and these affect their fitness. If households farm then this affects the production of seeds (through tree clearance). They assume seed harvest has diminishing returns, since the more a household collects the further they have to travel to get more, and farming produces constant returns.

Seed density, s, changes with time, t, according to

$$\frac{ds}{dt} = r_s p - d_s s - N h_s, \tag{2.4}$$

and tree density, p, changes according to

$$\frac{dp}{dt} = r_p s(1 - \frac{p}{K_p}) - Nc, \tag{2.5}$$

where r_s is the intrinsic production of seeds, d_s is the depletion rate of seeds by plants and decay, N is the density of households, h_s is the per capita harvest of seeds, $r_p s$ is the intrinsic growth of trees, K_p is the tree growth limiting effects by intraspecific competition and c is the land cleared of trees because of farming. Their model has a total of 12 parameters.

Their model has several stable states when households try to allocate their effort optimally. One of these states is productive and the other is impoverished; because of this the households run the risk of flipping from the productive to the impoverished. They find that in the short term farming can be optimal, but this can be sensitive to population density increases or decreases in wild resource productivity and hence in the longer run farming can be risky.

Bowles and Choi (2013)

In an agent-based game-theoretical model by Bowles and Choi (2013) the relationship between the advent of farming and farming-friendly property rights was studied. Their model was calibrated with a measure of climate volatility and their simulations showed the coevolution of farming and farming-friendly property rights at approximately the same time as may be expected from the archaeological record.

I replicate and analyse this model in Chapter 3, and thus I will fully describe it there.

2.3.3 Summary

These models predict the importance of various factors on the transition to agriculture. The work of Wirtz and Lemmen (2003), Dow and Reed (2011) and Marceau and Myers (2006) suggests that technological innovation could have been an important factor for the transition – via the decline in cooperation in the case of Marceau and Myer's model. Locay (1989) and Dow et al. (2009) suggest that population pressure could have caused the transition to agriculture, perhaps via sedentism in the case of Locay's model. On the other hand, Wirtz and Lemmen (2003) suggest that population pressure was not a key factor for the transition. Declining cooperation and the emergence of property rights are shown to be important for the switch in the model by Bowles and Choi (2013). Climate change is also seen to play a part in the transition for the models in Dow et al. (2009), Dow and Reed (2011) and Bowles and Choi (2013), however, the model by Wirtz and Lemmen (2003) predicts that the transition would still have occurred (albeit later) without climate fluctuations.

These models all highlight how modelling can be a critical tool for understanding why behaviours and practices might change. Even though there are contradictions in some results and differences in what processes and parameters people choose are important to include or exclude in their models, these models provide a way to test hypotheses. Inspired by several of these models – notably those by Freeman and Anderies (2012), Locay (1989), Bowles and Choi (2013) – I create a new evolutionary model for the origins of farming. This model includes certain factors which I think are critical to understanding why subsistence behaviour changed (based the literature reviewed in Chapter 1), but to my knowledge have not been included together in a model before. These factors are subsistence and mobility decision making, population size variation, resource quality variation, and a dynamic human-environmental interaction.

As in Anderies and Hegmon (2011), Freeman and Anderies (2012) and Dow and Reed (2015) in my model I look at movement decisions in an environment with resource variability. However, unlike these, I also include the possibility that people can farm. The models I have looked at do not include both farming and mobility, apart from Locay's (1989), but in this there is a uniform environment. In my model the environment responds to the human population as in Freeman and Anderies (2012), and environmental quality is not solely determined by climate data as it is in Wirtz and Lemmen (2003) and Bowles and Choi (2013). Furthermore, there is no explicit link between mobility and subsistence strategies as there is in Locay (1989) – the optimal behaviours in my model are able to evolve. A full comparison of the models reviewed in this section and the factors I include in my model is shown in Table 2.3.

Table 2.3: Motivation for a new model for the origins of agriculture. A checklist of whether the models reviewed in this section contain elements from the models I develop in Chapters 4 and 6.

	Mobility decisions	Subsistence decisions	Population size variation	Resource quality variation	Human-environment dynamics
Anderies and Hegmon (2011)	✓		✓	✓	✓
Freeman and Anderies (2012)	✓		✓	✓	✓
Dow and Reed (2015)	✓		✓	✓	
Hamilton et al. (2016)	✓		✓		
Locay (1989)	✓	✓	✓		✓
Wirtz and Lemmen (2003)		✓	✓	✓	✓
Marceau and Myers (2006)		✓			
Baker (2008)		✓	✓	✓	✓
Dow et al. (2009)		✓	✓	✓	
Dow and Reed (2011)		✓	✓		
Freeman et al. (2015)		✓			✓
Bowles and Choi (2013)		✓		✓	

2.4 Methodological Contributions

In this section I will describe the analysis methods I have developed. In Section 2.4.1 I will describe the fitting to idealised outcomes (FIO) approach; in Section 2.4.2 I will describe an algorithm for predicting when model outcomes change; in Section 2.4.3 I will describe a method of measuring convergence in simulation outcome distributions; and in Section 2.4.4 I will describe a method to infer parameter-outcome associations and simulation outcome types (the Outcome Clustering method). These methods are particularly useful for stochastic models where every run of the model can yield different outcomes, and/or in models where exact parameter values are unknown and therefore the parameter space needs to be explored.

2.4.1 The FIO Approach

As mentioned in Section 2.2.4 the fix-all-but-one approach is commonly used in the parameter sensitivity analysis of models. I will illustrate this approach using a basic model for population growth. I will also use this model to introduce the fitting to idealised outcomes (FIO) approach, which tests parameter sensitivity amongst other things.

Population growth can be modelled according to the exponential growth equation

$$n_t = n_{t-1}(1 + r) = n_0(1 + r)^t, \tag{2.6}$$

where n_t is the population size at t years, r is the maximum per capita growth rate and n_0 is the initial population size.

If the purpose of this model was to find the population size after 10 years (n_{10}) but there were no exact values for n_0 and r, I could vary both n_0 and r and find n_{10} for every combination. This can be seen in the top left panel of Figure 2.3, where r is varied in the x-axis and n_0 is varied in the y-axis. Thus in this simple two parameter model the sensitivity of the parameters and parameter interactions can be explored relatively easily.

If I then add more complexity to this model and allowed there to be a death rate, the model becomes slightly more difficult to analyse. For this I model the population growth as

$$n_t = n_{t-1}(1 + r - d) = n_0(1 + r - d)^t, \tag{2.7}$$

where d is the death rate of the population. I can still visualise how these parameters

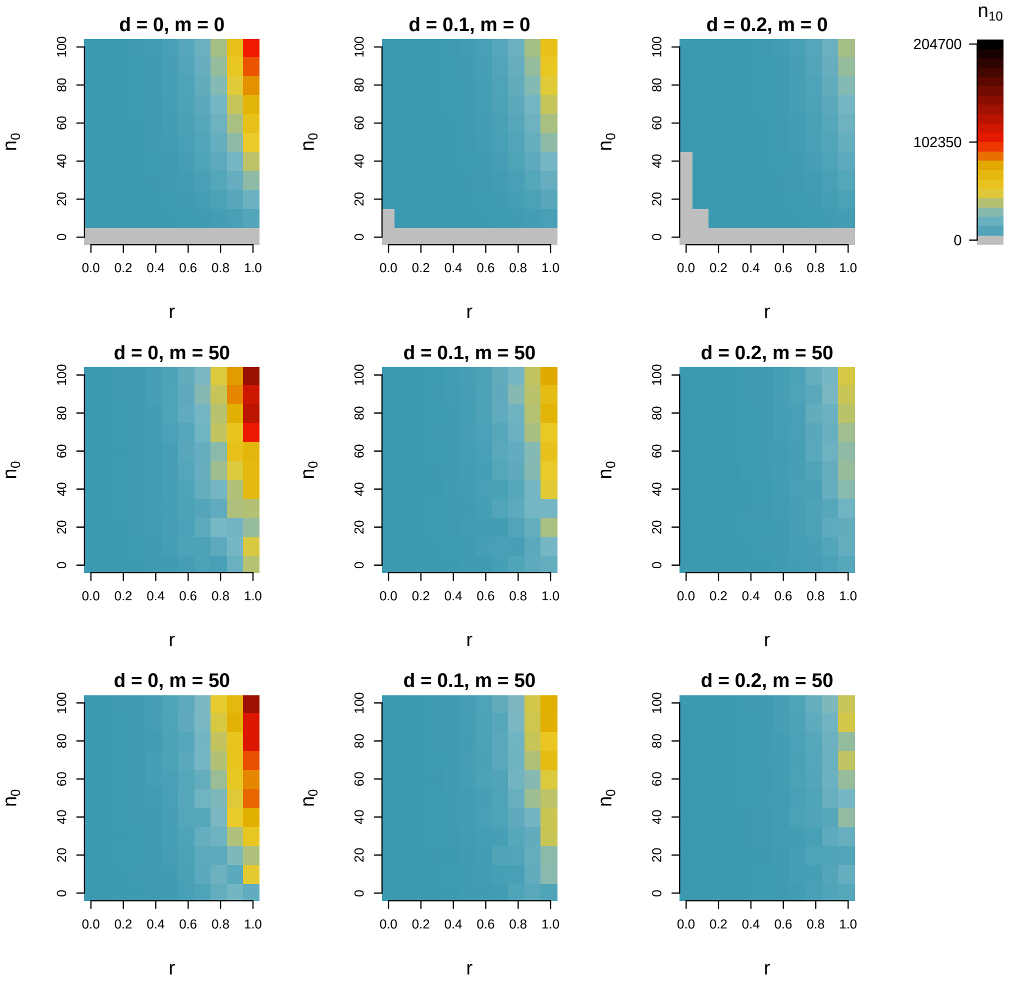


Figure 2.3: Population size after 10 years, n_{10} (colour – see key) when looking at different combinations of the four parameters.

affect the population size after 10 years in 2D, but now one of the parameters cannot be varied continuously, and thus the parameter interactions are less easily examined. This is shown in the top row of Figure 2.3, where I have investigated the effect of changing d.

I now add a fourth parameter to the model, m, which stochastically models migration. I pick the number of people migrating into the population every year from an uniform distribution between 0 and m, hence

$$\begin{aligned} M &\sim \mathcal{U}([\,0, m]\,) \\ n_t &= n_{t-1}(1 + r - d) + M, \end{aligned} \tag{2.8}$$

The top 2 rows of Figure 2.3 show how we can vary all four parameters and visualise the outcome, but now two of the parameters cannot be varied continuously and parameter interactions become even more complicated to analyse. Since the addition of migration means that there is now a stochastic element, each run of the model will now have slightly different outcomes – this can be seen by comparing the middle and bottom rows of Figure 2.3 where the parameters were kept the same.

Thus with increasing model complexity (and in this example there are only 4 parameters) the effects parameters have on the outcomes of a model can become progressively more difficult to analyse. Varying one parameter at a time to explore parameter sensitivity also relies on having a default value to set the other parameters to, but there is not always the data available to find this value. However, if there is data which suggests that only a small range of values are realistic (but there is no exact value known) then complexity will be reduced.

If we assume (perhaps by some intuition from data) that the default values for each of these parameters are $r = 0.55$, $n_0 = 10$, $d = 0.45$ and $m = 50$[1], we can see how varying each parameter in turn affects the number of agents after 10 years. This is shown in Figure 2.4. Using this approach I can get an idea of how each parameter affects the outcomes, however since the model has stochastic elements to it the results will be different each time.

This method provides a one-dimensional view of the parameter complexities, since it has possibly relied on ill defined default values and has not accounted for the variation in these results every time the models are run. Unfortunately this is the method often used to study the effects of model parameters. However, another method can provide a more detailed view. This method will be referred to as ‘fitting to idealised outcomes’ (FIO), and it is very similar to approximate Bayesian computation (ABC) (Beaumont,

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[1] These values are entirely made up for illustrative purposes.

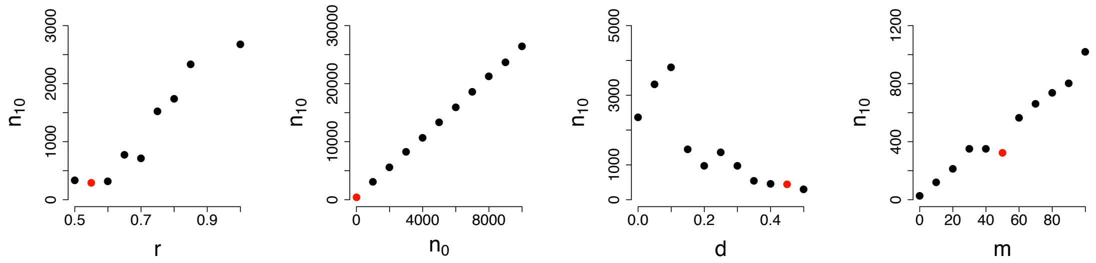


Figure 2.4: Population size after 10 years (n_{10}) when varying each of the four parameters in turn and keeping the others at their default values. Default values are shown in red.

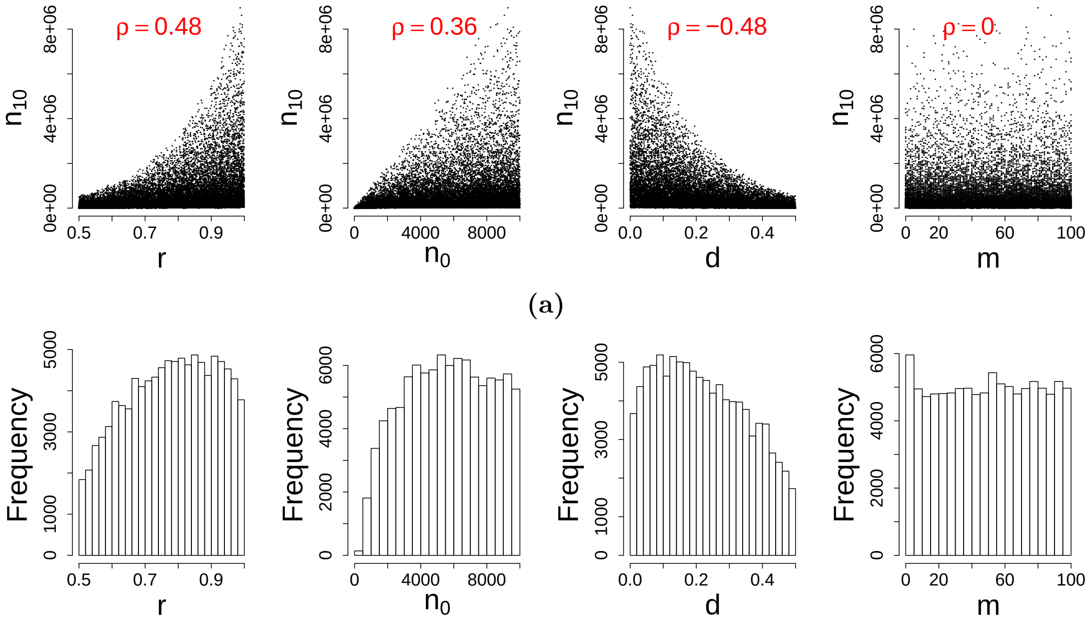
2010).

FIO has three steps:

1. Many simulations of the model are run with random combinations of parameters – this allows trends between the parameters and the outcomes to be seen, as well as studying parameter interdependencies and sensitivity.
2. An idealised outcome is decided on. This is informed by observed data.
3. Simulations which give the most ideal outcome are then separated out. The parameter value combinations which were used in these are interpreted as being most likely to cause the ideal outcome.

This process differs from in ABC in step 3. In ABC summary statistic(s) from observed data are compared to the same summary statistic(s) from the modelled data, rather than a simple comparison of basic outcomes. Thus in ABC the comparison of the simulation and observed data is much more robust, and thus ABC can be used to infer parameters and validate complex models. However, to do this ABC relies on having detailed observed data which is not always possible. Thus, I propose that when observed data is not rich enough to allow ABC, but either some general outcome is known or is of interest, FIO is a good method for studying parameter sensitivity and model behaviour with much more detail than the fix-all-but-one approach allows.

Using the FIO method in my population growth model I can look at the relationship between parameter values and the population size after 10 years. I run the model 100,000 times with different parameter values (step 1). From this it can be seen which parameter values cause certain values of n_{10} in 100,000 simulations of the model; these relationships are shown in Figure 2.5a.



(a)

(b)

Figure 2.5: Results from applying the FIO method. (a) The relationship between parameters and the population size after 10 years (n_{10}) in 100,000 simulations. Pearson's product moment correlation coefficient, ρ, between the parameter value and population size after 10 years is shown in red. (b) The frequencies of parameter values in the 1% of simulations closest to having $n_{10} = 400,000$.

If my observed data suggests that the actual population size after 10 years is 400,000, I then look for the simulations which are closest to this (the 'top simulations'). $n_{10} = 400,000$ is therefore my idealised outcome (step 2). The parameter value distributions in these top simulations are shown in Figure 2.5b (step 3). In ABC these would be the posterior distributions.

Hence, my interpretation from this analysis could be that in the range I looked at the upper limit on the number of people migrating in, m, makes little difference to the overall population size after 10 years. High values for the growth rate and initial population size, and low death rates, cause higher population sizes over time. I can also estimate which parameter values might be likely to cause the observed outcome by looking at the modes of the histograms in Figure 2.5b.

There is much more analysis and statistical tests which can be done on the data collected from implementing the FIO method. These will be explored in context when I use the FIO method in my model analysis in Chapters 3 and 6.

2.4.2 Predicting When Outcomes Change

In an evolutionary model there may be an outcome (for example cooperative behaviour or population size) of the model which changes over time. There may be a period of time when this outcome changes by random drift, and then there may be a selection pressure which means that the outcome evolves towards a particular value.

If there are multiple outcomes changing in this way, it is often of interest to be able to quantify the point at which when they change in order to be able to estimate the order in which events happened (for example does the evolution of cooperation happen before an increase in population size or after?). In some cases predicting which outcome changes first could be done by simply looking at a plot of the changes over time. However, being able to quantify this rather than a prediction by eye is useful when evaluating this consistently for many simulations. I have developed an algorithm to predict when this point of change occurs.

The way I quantify the point of change is by fitting a linear model (line of best fit) to the outcome values in the first 100 time points (or any other block size) and comparing the gradient of this slope to that of the next block of 100 points (e.g. compare an outcome for time points 1 to 100, and 101 to 200). I then perform a two-tailed Student's t-test on these two sets of fitted data points, where my null hypothesis is that the slope of the first block is equal to that of the second block. With a p-value threshold of 0.01 I reject or accept the null hypothesis. I then calculate the point of change as the first time point of the second block when the null hypothesis was rejected, i.e. the slopes were significantly different. Examples of the point of change predicted by my algorithm in two outcomes are shown in Figure 2.6, it can be seen from these that Outcome 1 is always predicted to change before Outcome 2.

I can choose different block sizes, but there is a trade off since if the block size is too small it is very sensitive to the random oscillations which occur often, but if it is too big then the resolution of results will be low. By simply looking at a sample of the points of change predictions using different block sizes by eye, I can find a block size that gives the best results.

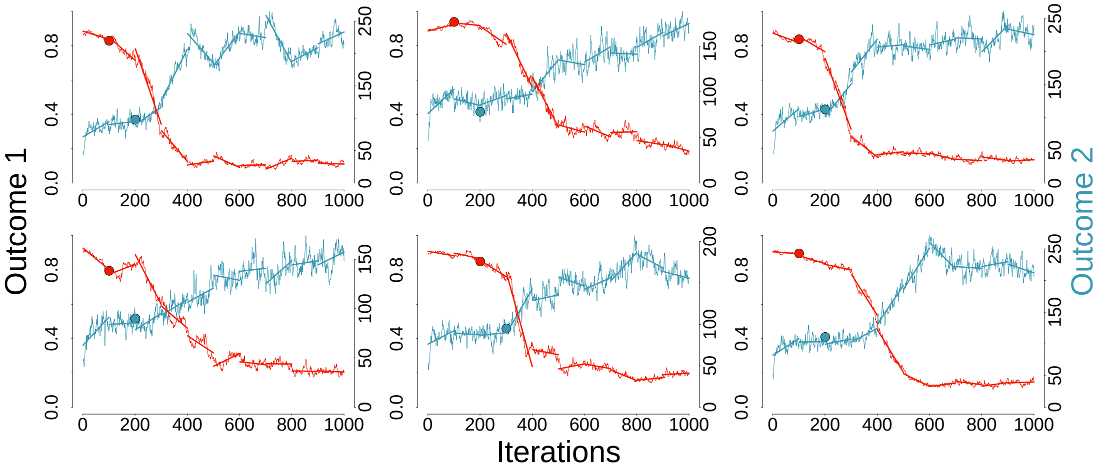
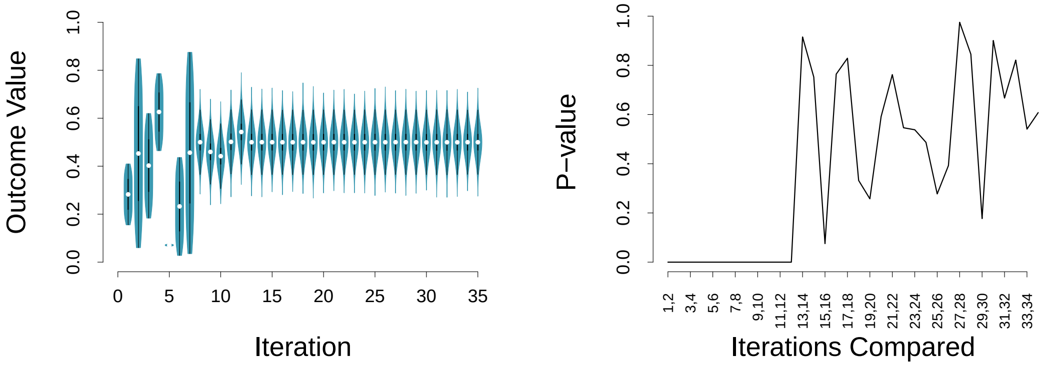


Figure 2.6: Examples of predicting the point at which two outcomes (‘Outcome 1’ and ‘Outcome 2’) start to change significantly (red and blue circles respectively). Lines of best fit for each 100-point window of results are also plotted.



(a) **(b)**

Figure 2.7: An example of measuring the point at which distributions become similar. (a) Violin plots of 100,000 values at each iteration (data was made up for illustrative purposes). (b) The p-values from a two-tailed Student's t-test on value distributions from two consecutive iterations. e.g. I perform a t-test on the values at iteration 1 and 2 and plot the p-value.

2.4.3 Measuring Convergence in Simulation Outcome Distributions

As well as finding the point at which an outcome starts to change more significantly than it does by drift (as I looked at in Section 2.4.2), it is also of interest to see when (and if) the changes in the outcome value have stabilised. In terms of simulation modelling this point is useful to know since it may be the case that running the simulation for longer will not result in any differences in results, but will take up time and processing power. However, caution must be taken since some systems may stabilise but then they might begin to change again.

If many simulations of the model are run over many iterations then there will be a distribution of outcome values for each iteration. These are shown using made up data in Figure 2.7a. From this plot it can be seen that the outcome value distributions become quite similar after iteration 13. I can measure convergence more quantitively by performing a two-tailed Student's t-test between the outcome distributions at consecutive pairs of iterations (e.g. comparing the distributions at iteration 1 and 2). If the p-value of these tests is big then I cannot reject the null hypothesis that the distribution means are equal. I plot the p-values for each consecutive outcome distribution in Figure 2.7b. Indeed, the p-values become large (> 0.01) after iteration 13; indicating that the distribution means are likely to be converging at this point.

2.4.4 The Outcome Clustering Method

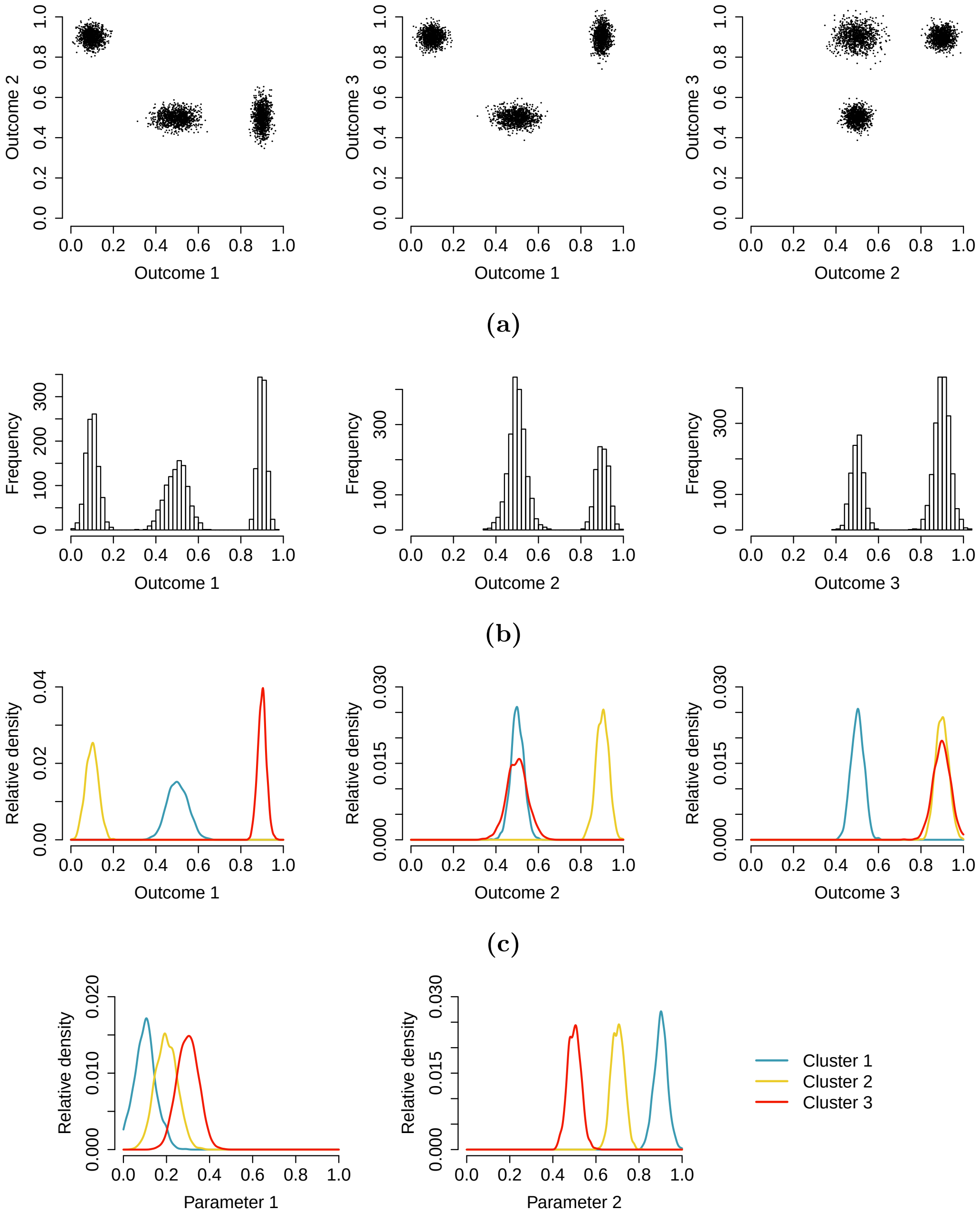
In the FIO example in Section 2.4.1 the outcome of the model was population size, and I found that a combination of specific parameter values made it most likely for a particular idealised outcome to occur. There may also be other outcomes of a model and it may be of interest to see if there are any relationships between different outcome values. For example, outcomes of high population size and high gross domestic product (GDP) may co-occur in the model.

When there are multiple outcomes of the model a simple correlation coefficient could be found to see relationships. However, correlation coefficients would not pick up on any granularity in the specific outcome values which may co-occur together, especially if the relationships are not strictly linear. I propose another method where outcomes are clustered to find any relationships between them. I will refer to this method as the Outcome Clustering (OC) method.

For this method many simulations of the model are run, and outcomes are recorded. I then use the function 'Mclust' in the R library 'mclust' (Fraley and Raftery, 2002; Fraley et al., 2012; R Core Team, 2013) to find clusters of simulations on the basis of their outcomes. After identifying these simulation clusters the distributions of the parameter values in each cluster can be found.

To illustrate this method I have made up the parameter and outcome values (where there are two parameters and three outcomes) of 3000 simulations. Figure 2.8a shows scatter plots of each simulation outcome pair and Figure 2.8b shows the frequency distributions for each outcome. From these figures there are clear clusters in the outcomes, and indeed the clustering algorithm in R identified three clusters. Using the cluster classifications found I can look at both the relative densities of outcomes and parameters in each of the three clusters (Figure 2.8c and 2.8d respectively). In this example these figures show how certain parameter ranges are associated with quite distinct outcome types.

The data I made up for this example had very clear and distinct outcome clusters, however this might not always be the case. Thus, this method systematically identifies differences in simulation outcomes and whether certain parameter values are associated with outcome types.



(a)

(b)

(c)

(d)

Figure 2.8: An example of using the outcome clustering method to infer parameter-outcome associations and simulation outcome types using made up data. (a) Scatter plots of each pair of the three outcomes. (b) The frequencies of the three simulation outcome values. (c) The relative densities of the three simulation outcome values in each of the three clusters identified. (d) The relative densities of the two parameter values in each of the three clusters identified.

Table 2.4: A summary of how I use the data reviewed in this section. When the data is used for parameter fitting I have included the parameter symbols – see Tables 3.2 and 6.2.

Data Source	Use Type	Value
Kelly's (2013) hunter-gatherer mobility data	Model validation	There is an exponentially decreasing relationship between reduced mobility and larger population density
Kelly's (2013) hunter-gatherer mobility data	Model validation	There is less mobility in areas where there is more to eat
Kelly's (2013) hunter-gatherer population density data	Parameter fitting	The maximum number of agents which can be supported at a site, n_{max}
Mace's (1996) Gabbra wealth and fertility data	Parameter fitting	There is a logarithmic relationship between wealth and fertility, $p(f)$
Kelly's (2013) hunter-gatherer fertility and mortality	Parameter fitting	The upper fission probability, p_{max}
Archaeobotanical data	Model validation	The timings of when agriculture became adopted in SW Asia
Bocquet-Appel's (2011b) population density data	Parameter fitting	How many more farmers can be supported than foragers, ϕ
NGRIP climate data	Parameter fitting	The disadvantage of farming due to temperature volatility, θ

2.5 Data

The first step in building a model is to consider what data is available. Thus in this section I will review and analyse the ethnographic, archaeological and climate data I use to inform my model decisions, fit parameter values, and validate the model. Reference back to the data in this section will be made when I describe my model in Chapter 4 and Section 6.1.

As mentioned in Section 2.2.4 data is used fit model parameters and to validate the model, but the same data should not be used for both. An overview of which data is used for these purposes is given in Table 2.4.

I did not collect any of the data presented in this section, however the data cleaning, merging and analysis is my own contribution. This is with the exception of the Gabbra household wealth-fertility relationship by Mace (1996) which is simply reviewed.

2.5.1 Ethnographic Data

A large dataset of information about hunter-gatherers from all over the world is provided by Kelly (2013). This data includes details of hunter-gatherer mobility behaviour, population density, group sizes, fertility and mortality rates, and the environments in which the groups live. In this section I will discuss this data along with the relationship between fertility and wealth given by Mace (1996). I include some details of the data cleaning I had to do, and give the datasets used, in Appendix A.

Mobility

A summary of part of the dataset on hunter-gatherer mobility (Table 4-1 in Kelly, 2013, p.80–84) is given in Table 2.5. The variables included in this data are the number of residential moves per year, the average distance moved each time, the total distance moved and area used in a year, and the average number of days a logistic move takes. Also included in this Table is a measure of food availability (primary biomass) and population density. After cleaning this dataset (details to which are given in Appendix A) there were 87 hunter-gatherer groups included, although there are not always values available for each variable. How these variables vary in different region types (e.g. Arctic, Temperate forests) is shown in Figure 2.9. It can be seen that these values vary widely, where some of the variation can be explained by region type.

The relationship between how often hunter-gatherer movement occurs (residential moves per year) and other factors is shown in Figure 2.10. For these the biggest correlation is with the total distance moved per year. Kelly's dataset also shows that the number of residential moves per year exponentially decays with increasing population density – shown in Figure 2.11a. Furthermore, Kelly finds as primary biomass increases so do the number of residential moves – shown in Figure 2.11b. Primary biomass is defined as "an environment's total amount of standing plant matter" (Kelly, 2013, p. 85), where high primary biomass means the plants invest more in structural parts of the plants, and less in seeds/nuts/tubers etc. Therefore there can be less for foragers to eat in areas of high primary biomass.

Dependence on aquatic resources and residential mobility are negatively correlated (Kelly, 2013, p. 92) – see Figure 2.12a. A further trend is that generally hunter-gatherers in higher effective temperatures tend to be more nomadic, but also those from the lowest (the arctic) are highly mobile (Binford, 1980), see Figure 2.12b.

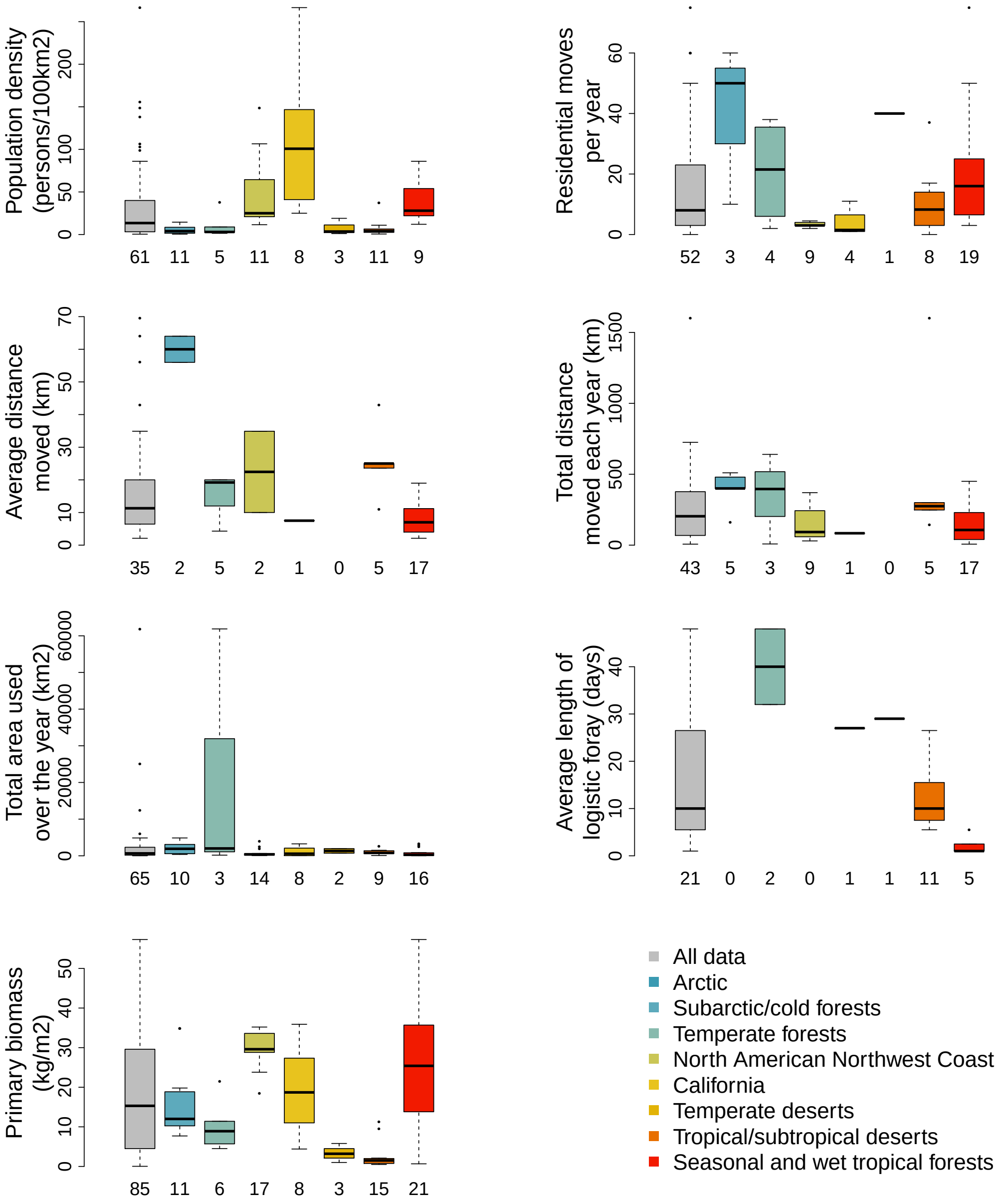


Figure 2.9: Box plot summaries of Kelly's hunter-gatherer mobility data separated into region type, sample size shown underneath. Data from Kelly (2013, p.80–84) (Table 4-1).

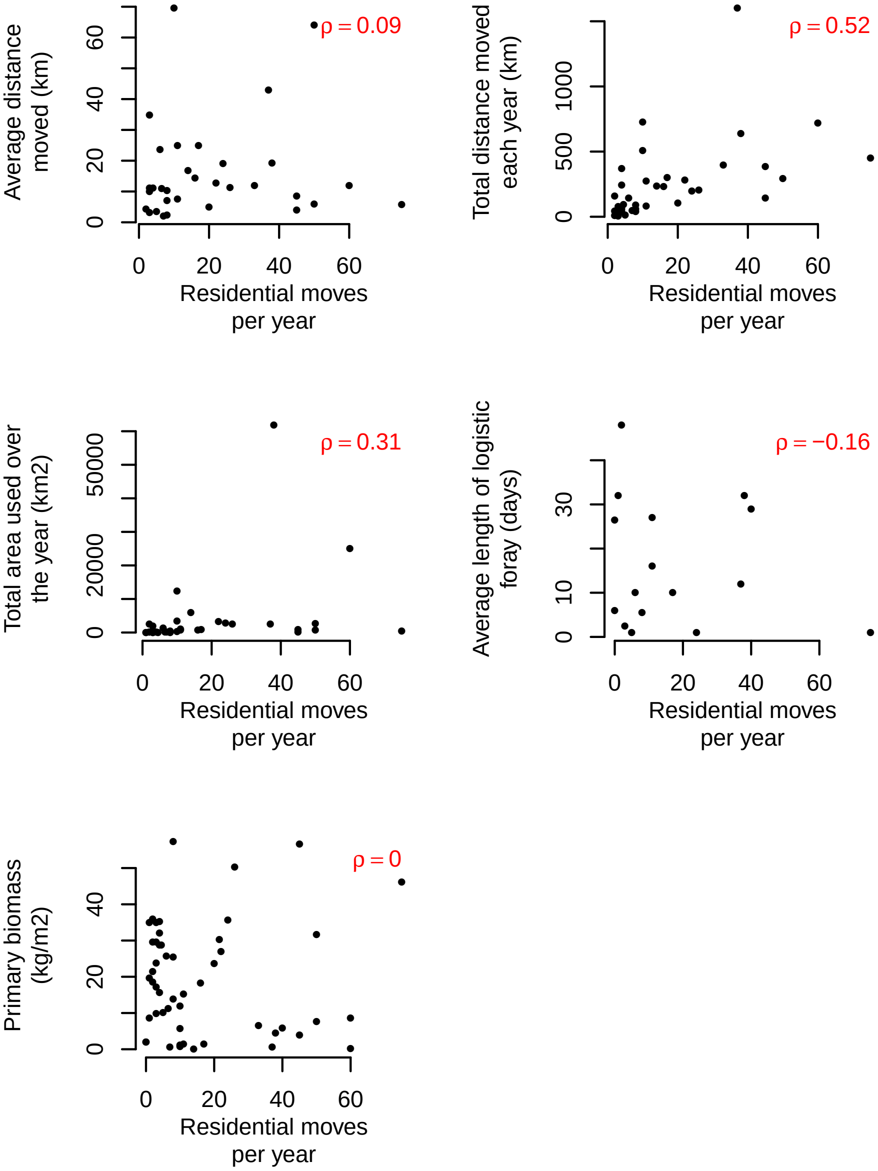
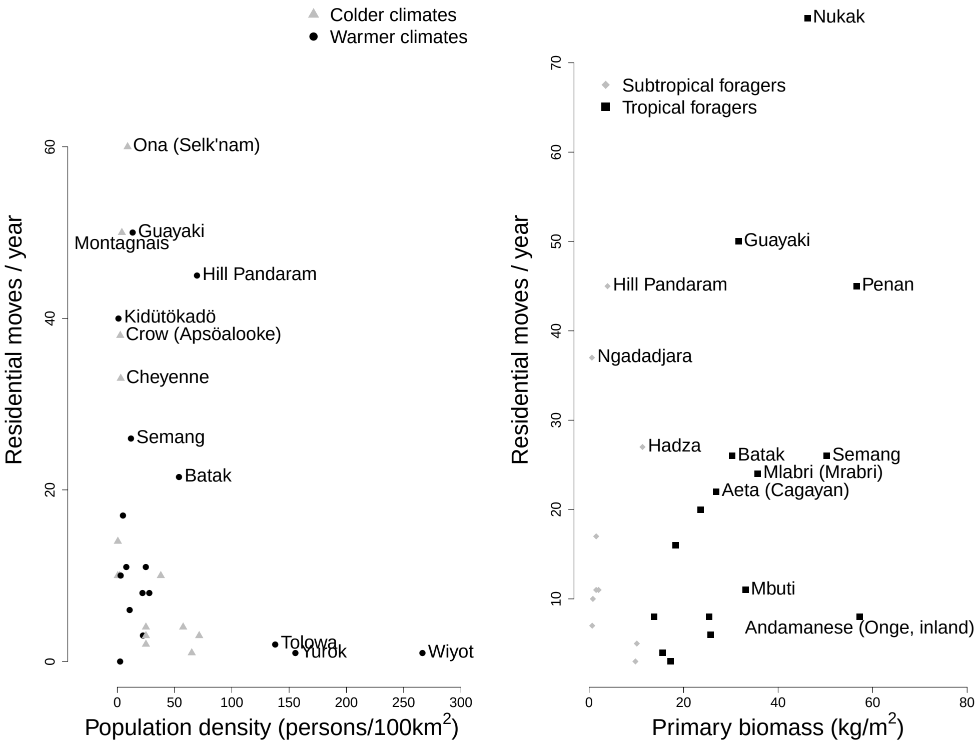


Figure 2.10: Relationships between the number of residential moves per year and other hunter-gatherer mobility variables recorded in Kelly (2013, p.80–84) (Table 4-1). Pearson's product moment correlation coefficient, ρ, is given in red in each plot.

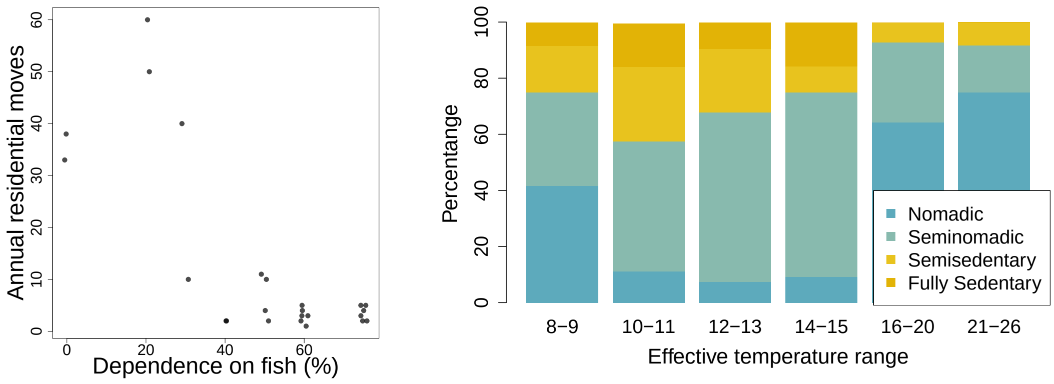


(a) **(b)**

Figure 2.11: Hunter-gatherer residential mobility, density and primary biomass. (a) Number of residential moves per year against the population density (persons per 100 km^2) for 31 forager groups. Point style denotes whether the groups live in relatively colder or warmer climates (colder climates are from the area categories 'Arctic', 'Sub-arctic/cold forests', 'Temperate forests', 'North American Northwest Coast', with the other area categories defined as warmer climates). Pearson's rank correlation coefficient for all the data points is $\rho = -0.33$, with a p-value of 0.071; for just the colder climate foragers $\rho = -0.56$, with a p-value of 0.039; and for just the warmer climate foragers $\rho = -0.31$, with a p-value of 0.22. (b) The number of residential moves per year against the primary biomass for the 26 tropical and subtropical forager groups. Reproduced from Kelly (2013, p.88) (Figure 4-4). Pearson's rank correlation coefficient for all the data points is $\rho = 0.37$, with a p-value of 0.066; for just the tropical foragers $\rho = 0.51$, with a p-value of 0.043; and for just the subtropical foragers $\rho = -0.12$, with a p-value of 0.73. The data used to make these plots is from both Kelly (2013) and private correspondence with Robert Kelly.

Table 2.5: Summaries of the cleaned data collected by Kelly (2013) on the mobility, primary biomass (Table 4-1, pg. 80–84) and population density (Table 7-3, pg. 178–184) of hunter-gatherers, given in Appendix A.

	Number of groups	Mean	Minimum	Maximum	Standard deviation
Residential moves per year	52	16.5	0	75	18.7
Average distance (km)	35	17	2.1	69.5	17
Total distance (km)	43	262.6	7	1600	283.0
Total area (km^2)	65	2646.8	8.0	61880.0	8241.6
Logistic mobility (days)	21	15.3	1	48	13.1
Primary Biomass (kg/m^2)	85	17.9	0	57.3	14.9
Population density (persons/100km^2)	70	34.2	0.4	266.5	47.1



(a)

(b)

Figure 2.12: Movement, dependence on fish and effective temperature. (a) Annual residual moves and the dependence on fish for several hunter-gatherer groups, data from Kelly (2013, p.92) Table 4-3. (b) Settlement-patterns and effective temperate range. Bars show the six different ET ranges, split into the proportion of each of four types of settlement-pattern. Data from Binford (1980) Table 2.

Table 2.6: Summaries of the cleaned data collected by Kelly (2013) on the group sizes (Table 7-2, pg. 171), mortality (Table 7-7, pg. 201) and fertility (Table 7-5, pg. 195–196) of hunter-gatherers, given in Appendix A. Mortality here is the percentage of people under 1 or 15 years who die, and total fertility rate is the number of children that would be born per woman if they survive through childbearing years.

	Number of groups	Mean	Minimum	Maximum	Standard deviation
Group Size	34	143.0	13.5	1500.0	288.6
Group Size (Nomadic)	19	29.1	13.5	61.0	12.7
Group Size (Sedentary)	15	287.2	33.0	1500.0	395.3
Mortality (%) <1yr	16	20.8	8.0	37.0	9.3
Mortality (%) <15yr	27	35.3	6.0	61.0	15.0
Birth Interval (months)	15	5.6	2.3	37.6	8.9
Total Fertility Rate	52	5.7	2.6	8.5	1.4

Group Size, Fertility, Mortality and Wealth

Kelly (2013) also gives data on group sizes (Table 7-2, pg. 171), fertility (Table 7-5, pg. 195–196) and mortality (Table 7-7, pg. 201) of various hunter-gatherer groups, this data is shown in Appendix A. This data is summarised in Table 2.6 and in Figure 2.13. Figure 2.14 shows the pairwise relationships between the mortality rates of infants and adolescences, and between the birth interval and the fertility rate.

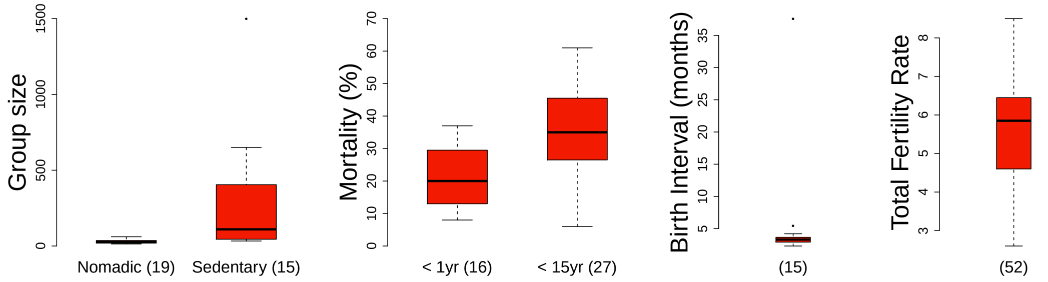
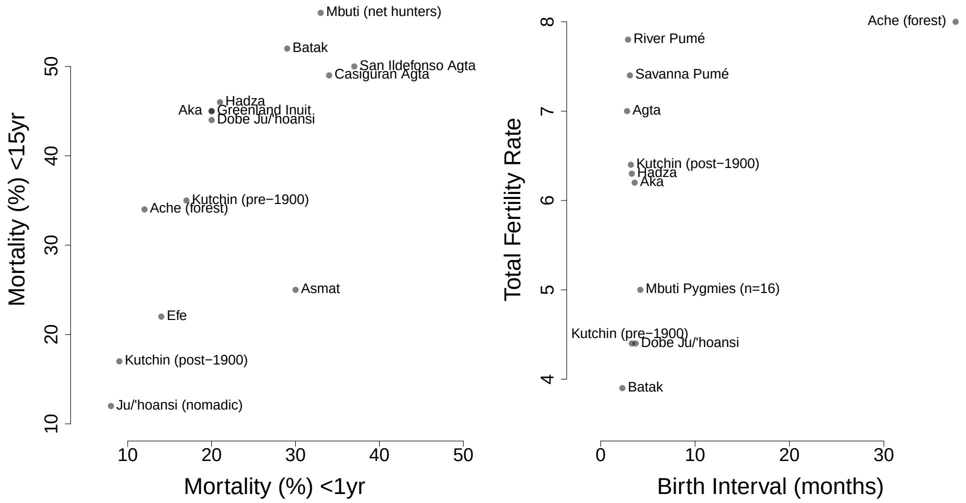


Figure 2.13: Box plot summaries of Kelly's hunter-gatherer group size, mortality and fertility data, from Kelly (2013) (Tables 7-2, 7-5, and 7-7). The number of groups in each sample is given in brackets.

In a study by Mace (1996) the relationship between wealth and fertility in the Gabbra nomadic pastoralists is investigated. The number of camels is used as a proxy for wealth and 848 households are included in the study. Mace found that the equations for the best fit regression curves are $-0.714 + 0.516 \log(\text{no.camels} + 1)$ and $-0.292 +$



(a) **(b)**

Figure 2.14: Scatter plots of Kelly's mortality and fertility data. (a) The relationship between mortalities of children under 1 year old and those under 15 years old in 14 hunter-gatherer groups (Pearson's rank correlation coefficient, $\rho = 0.74$, p-value $=$ 0.003). (b) The relationship between birth interval and total fertility rate in 11 hunter-gatherer groups ($\rho = 0.43$, p-value $= 0.18$). From Kelly (2013) (Tables 7-5 and 7-7).

$0.198 \log(\text{no.camels}+1)$ respectively for men and women's residual fertility (Mace, 1996). This result is reproduced in Figure 2.15.

Primary Productivity and Effective Temperature

Kelly (2013) also provides data on the environment of hunter-gatherer groups (in Table 3-1, pg. 41–43, data which is mostly taken from Murdock, 1967). There is a strong positive correlation between the primary productivity and effective temperature of the 126 hunter-gatherer groups, see Figure 2.16a. Furthermore the dataset also gives the percentage of food derived from three different activities, I have plotted these in Figure 2.16b.

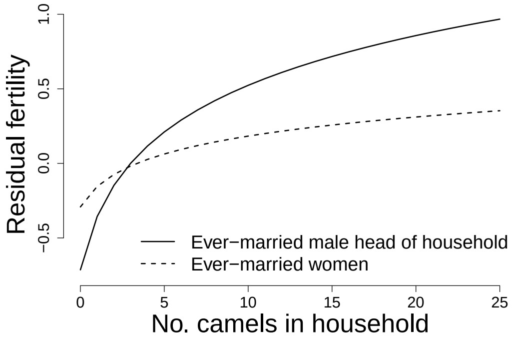
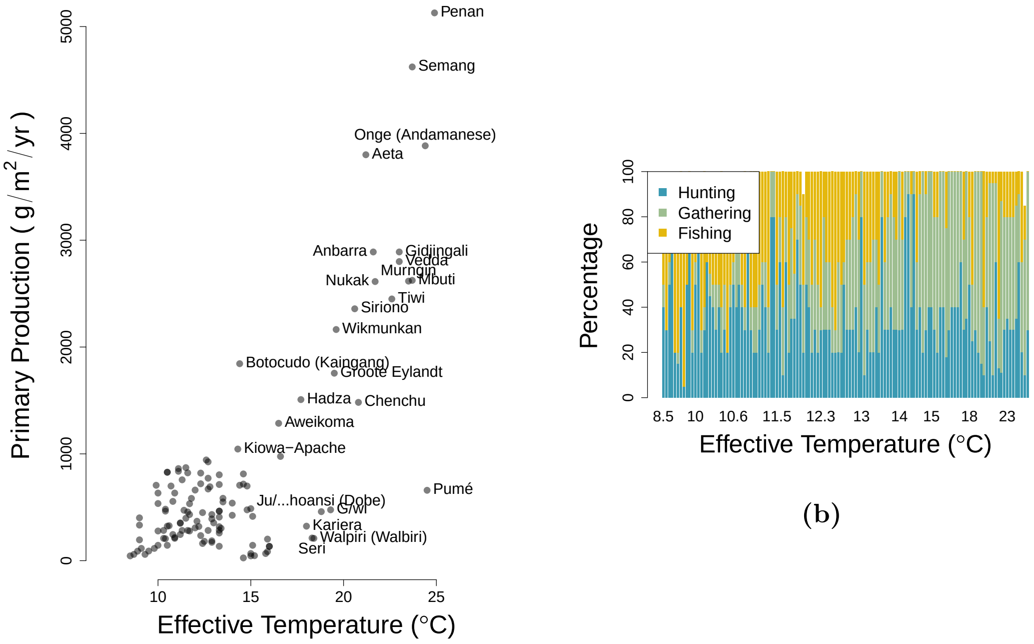


Figure 2.15: The relationship between wealth and fertility. The best fit regression curves of data on the number of camels in the household (a measure of wealth) and the residual fertility of ever-married male head of household (solid line) and ever-married females (dashed line), from a study by Mace (1996) on 848 Gabbra households. Reproduced from Mace (1996, pg. 77).



(a)

(b)

Figure 2.16: (a) The relationship between effective temperature and primary productivity in 126 hunter-gatherer groups (some group names are given). Pearson's product moment correlation coefficient, $\rho = 0.75$, where the p-value is 0.00. (b) Percentage of food derived from hunting, gathering and fishing separately in the 126 hunter-gatherer groups, ordered by effective temperature. Data from Table 3-1 of Kelly (2013, pg. 41–43).

2.5.2 Archaeological Data

I also have archaeological data available to me[2]. These datasets provide me with a proxy to estimate the rate of the transition to agriculture (through changes in the wild-to-domestic ratio) and sedentism (through the appearance of ground stone tools), and population density.

Archaeobotanical Data

I obtained a dataset from the Institute of Archaeology at UCL of the published records of archaeobotanical samples from SW Asia; discussion of an early form of this dataset has been published in Colledge et al. (2004). The dataset includes 911 seed/grain or chaff samples from cereals and pulses, with the culture they date from, whether they are from the wild, domestic or 'wild/domestic' phenotypes and their ubiquity score. The ubiquity score is the percentage of this sample type in the total samples found. The sites these samples came from can be seen in Figure 2.17a. The culture category 'PPNB' (Pre-Pottery Neolithic B) in this dataset is used when there is no specific designation for early (E), middle (M), late (L) or final (F); since this category is vague I have left out the 45 'PPNB' data entries from the analysis in this section.

Figure 2.18a shows the proportion of wild, domestic and 'wild/domestic' phenotypes in each culture ordered by approximate dates (see Tables 1.2 and 2.7). I also looked at the domestic-to-wild phenotype ratios over time in Figure 2.18b (right). Since the exact year for certain categories (e.g. 'EMPPNB') are not given I have grouped 'EMPPNB', 'MPPNB' and 'MLPPNB', and 'LPPNB', 'LPPNB, PN', 'L/FPPNB' and 'FPPNB'. Since the 'wild/domestic' phenotype is ambiguous, I have included the three different options for calculating the domestic-to-wild ratio.

From this data it can be seen that the proportion of domestic phenotypes increases over time. However the data is of a low resolution, so we can only say something about the overall trend of increase – which is roughly exponential.

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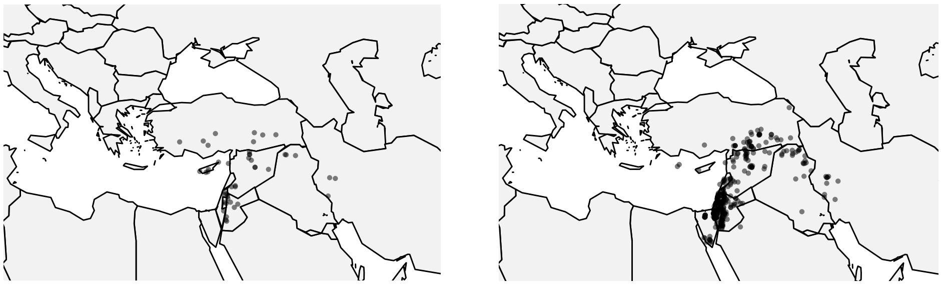
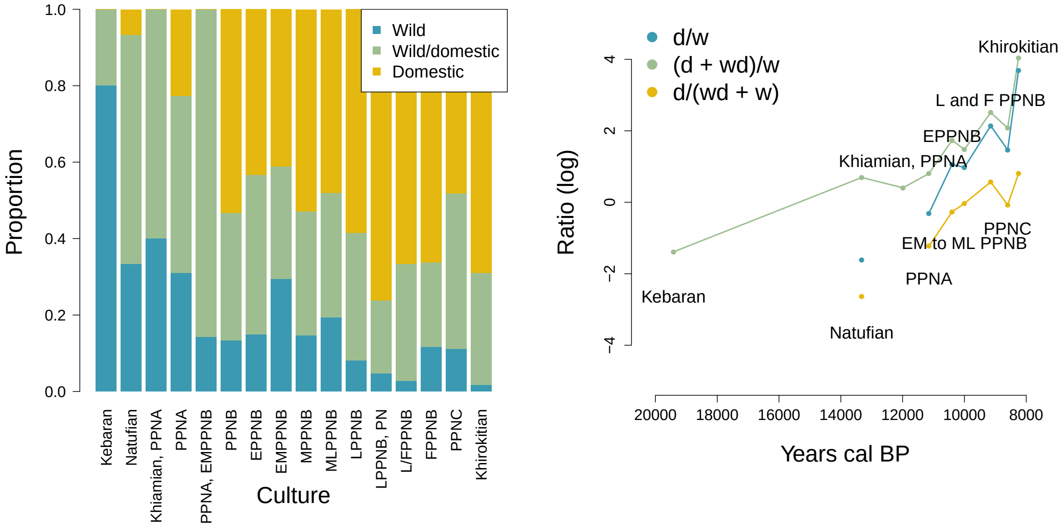
[2] Please correspond with Stephen Shennan for potential access to these datasets – s.shennan@ucl.ac.uk.



(a) (b)

Figure 2.17: Sites in SW Asia where the archaeobotanical dataset (left) and material culture dataset (right) come from.

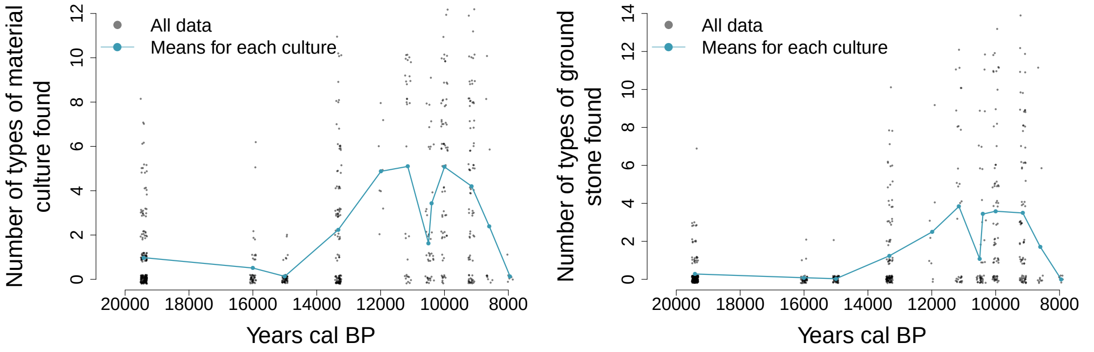


(a) (b)

Figure 2.18: Number of wild and domestic phenotypes over time. (a) The proportion of wild, wild/domestic and domestic phenotypes for each culture. (b) The three calculations of the domestic to wild ratios for different dates. ‘d’: domestic; ‘wd’: wild/-domestic; ‘w’: wild. The data points for ‘EMPPNB’, ‘MPPNB’ and ‘MLPPNB’ have been grouped, as have ‘LPPNB’, ‘LLPNB, PN’, ‘L/FPPNB’ and ‘FPPNB’, and a mid point in the period range has been plotted.

Table 2.7: Number of samples and date estimates from each culture category.

Culture classification	Number of samples	Mid-point cal BP estimate
Kebaran	5	19,413
Natufian	15	13,325
Khiamian, PPNA	10	11,988
PPNA	84	11,150
PPNA, EMPPNB	7	Vague culture classification
PPNB	45	Vague culture classification
EPPNB	60	10,400
EMPPNB	34	10,000
MPPNB	123	10,000
MLPPNB	150	10,000
LPPNB	123	9150
LPPNB, PN	21	9150
L/FPPNB	72	9150
FPPNB	77	9150
PPNC	27	8600
Khirokitian	58	8250



(a) **(b)**

Figure 2.19: How many of the different types of material culture (a; out of 12) or ground stone (b; out of 20) classifications each site had (points).

Material Culture

I also obtained an archaeological dataset which includes details of the material culture findings at 782 sites in SW Asia (for locations see Figure 2.17b) from the Institute of Archaeology at UCL. The dataset has presence/absence scores of various material objects (e.g. art, clay objects, ochre), but also burials/human remains and hearths. It also includes the number of different types of ground stone artefacts (e.g. grinding slabs, mortars). Having a large number of material culture types could be a proxy for sedentism, since the accumulation of items becomes possible when mobility is reduced (see Section 1.1.3).

The original data had 132 different classifications for the site's culture, however some of these were vague (e.g. 'Mixed Early/Late Epipalaeolithic and Neolithic') and/or only had one or two data entries for each classification. I reclassified the data into 14 different groups and did not include the vague data points. Figure 2.19a shows how many of the different types of material culture (out of 12 types) each of the 782 sites had present, where each site is grouped by the culture it belongs to. Similarly, Figure 2.19b shows how many of the different ground stone types (out of 20 types) each site had present. These plots show an increase and then a decline in the number of types of artefact.

Since the dataset only provides me with presence/absence scores for the material objects, and often very vague number of ground stone tool types (e.g. entries which say '>1' or 'many'), unfortunately I can only accurately infer how the range of types of these items increases over time.

Population Density

Through personal correspondence with Jean-Pierre Bocquet-Appel I obtained the dataset he analysed in Bocquet-Appel (2011b). This dataset includes the numbers of skeletons in different age ranges and the proportion of juvenile skeletons (5 to 19 years old), P_{5_19}, in 222 Northern Hemisphere cemeteries. The dataset also includes the difference in time between the advent of farming (dt) in each of the cemetery locations. The data has been used (Bocquet-Appel, 2011a,b) to illustrate the Neolithic demographic transition.

Bocquet-Appel (2011b) excludes cemeteries with low sample sizes, leaving 135 cemeteries – 32 from before farming and 103 after. This dataset includes skeletons with $dt \in [-7085, 3200]$ and the samples dated from 14,560 cal BP to 350 cal BP. Figure 2.20 shows the sites where this data is from, and Figure 2.21 shows how the number of skeletons and the proportion of juvenile skeletons increases after farming began.

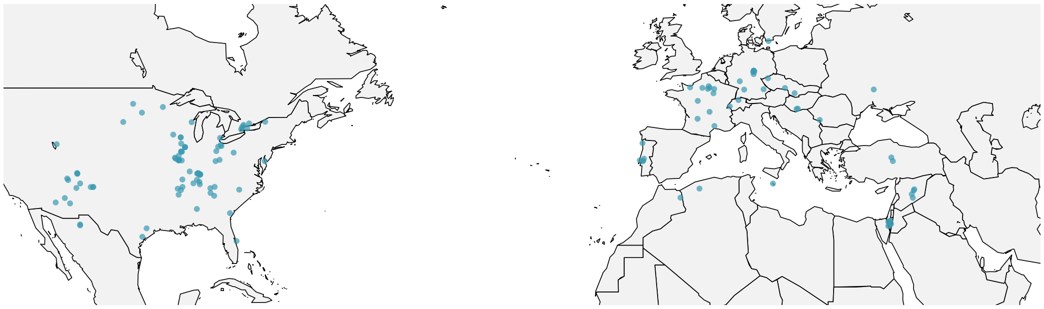
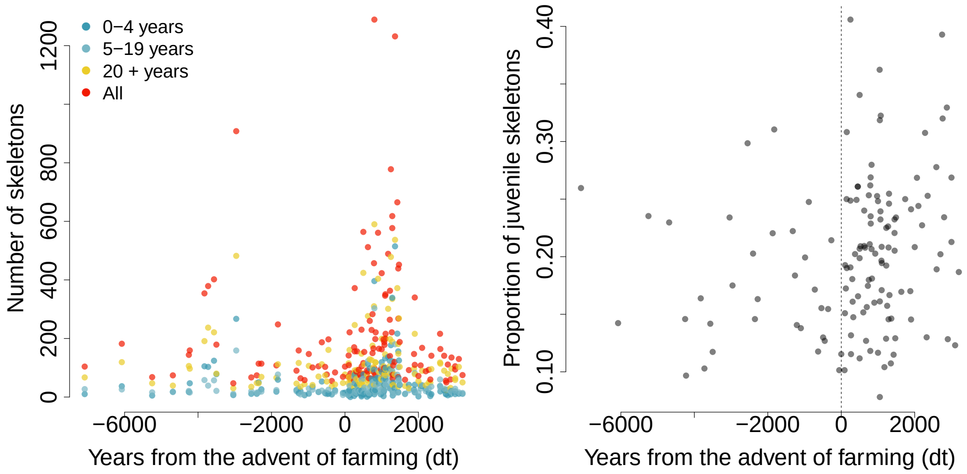


Figure 2.20: Cemetery locations in the dataset from Bocquet-Appel (2011b).

Table 2.8 shows the minimum, mean and maximum proportions of 5 to 19 year old skeletons before and after the advent of farming. The increase shown represents the increase in birth rate (and therefore fertility), but not mortality (Bocquet-Appel, 2011a). Thus, using this data I can find how many more people farming can support than foraging, $\Phi = P_{5\_19,after}/P_{5\_19,before}$. The maximum for this is $\Phi_{max} = 4.2$ and the average is $\Phi_{mean} = 1.17$.

I looked at these ratios in data with $dt \in [-y, y]$ with $y = [$ 500, 1000, 1500, 2000, 2500, 3000, 3500, 8000$]$, and the results are robust to changing the period of time around $dt = 0$ to include. All these ratios are shown in Table 2.9.



(a) **(b)**

Figure 2.21: Representation of the data from Bocquet-Appel (2011b). (a) The number of skeletons from different age ranges and (b) the proportion of 9 to 15 year old skeletons before and after the advent of farming.

Table 2.8: The minimum, mean and maximum proportion of 5 to 19 year old skeletons before and after the advent of farming in the data from Bocquet-Appel (2011b).

	Minimum	Mean	Maximum
Before the advent of farming	0.1	0.18	0.31
After the advent of farming	0.08	0.21	0.41

Table 2.9: Estimates of how many more people farming can support in comparison to foraging. Maximum and mean values for the ratios of 5 to 19 year old skeletons proportions before and after the advent of farming are found ($P_{5\_19,after}/P_{5\_19,before}$). Data from Bocquet-Appel (2011b).

dt period	Φ_{max}	Φ_{mean}
$[-500, 500]$	4.00	1.38
$[-1000, 1000]$	4.00	1.26
$[-1500, 1500]$	4.00	1.22
$[-2000, 2000]$	4.00	1.13
$[-2500, 2500]$	4.00	1.15
$[-3000, 3000]$	4.00	1.14
$[-3500, 3500]$	4.00	1.13
All	4.20	1.17

2.5.3 Climate Data

A high resolution paleoclimatic proxy is available in the form of the North Greenland Ice Core Project (NGRIP) (Andersen et al., 2006; Rasmussen et al., 2006; Svensson et al., 2006; Vinther et al., 2006). This data shows the ratio of stable isotopes oxygen-18 (^{18}O) and oxygen-16 (^{16}O), δ^{18}O, over the last 41,760 years (with a 20 year resolution) which can be used as a proxy for the temperature of ancient oceans. Figure 2.22 shows the values for $\delta^{18}O$ over time. This data shows how in the last 10,000 years the temperature has become more stable.

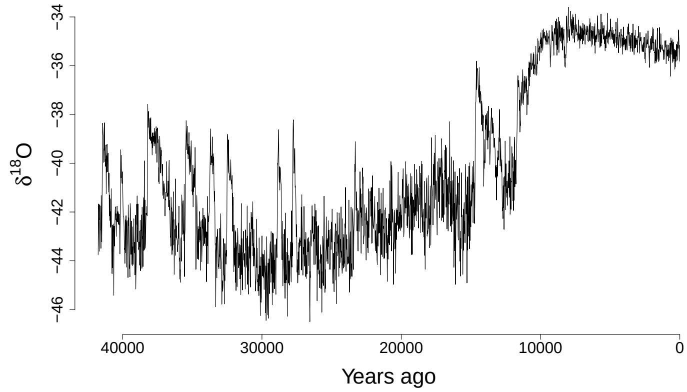


Figure 2.22: δ^{18}O over time from the NGRIP database (Andersen et al., 2006; Rasmussen et al., 2006; Svensson et al., 2006; Vinther et al., 2006).

Using this data as a proxy for temperature is very general. Thus incorporating climate data into a model of a region (for example SW Asia) would require more specific terrestrial climate data than this (for example the eastern Mediterranean continental paleoclimate determined from cave speleothems by Bar-Matthews et al., 1997). However, the NGRIP data shows general trends and by looking at the difference in δ^{18}O from decade to decade (or another resolution) a measure of climate stability can be found.

2.6 Conclusion

In the previous chapter I discussed how climate changes at the end of the Pleistocene were associated with changes in the way people lived. I showed how although it was not always through the same mechanisms or with the same timings, agriculture developed alongside becoming less mobile and increases in population size. In Section 2.3 I showed how modelling has been used to try to better understand the origins of agriculture, and in Sections 2.1 and 2.2 I showed how evolutionary theory, game theory and agent-based modelling can be used to study behaviour. In Section 2.4 I discussed some of the methods I developed in this thesis, and in Section 2.5 I reviewed and analysed the data I have available to develop my own model of the origins of agriculture.

In Chapters 4, 5 and 6 I will describe my evolutionary agent-based model which can be used to study the relationship between mobility and population size on the switch to agriculture. In this model, mobility and subsistence decisions are adaptable behaviours, where selection pressures are influenced by a dynamic and interacting population and environment.

Agent-based models have drawbacks; for example, if there are many parameters then checking parameter sensitivity can be complicated and computationally intensive, agent-based models can be very sensitive to initial conditions (and sometimes these are unknown), and in general, agent-based models can produce complex behaviour which can be complicated to analyse and understand. However, I think that my methodological contributions in this thesis can help significantly with these problems. Furthermore, the use of an agent-based evolutionary algorithm framework for what I want to model is appropriate for two reasons:

1. What I am modelling is inherently individual-based behaviours (mobility and subsistence strategies), and how these change over time.
2. The data I have available allows me to make predictions about individual dynamics (e.g. how fertility can be predicted from fitness), but not global (e.g. how population size changes over time).

Although my data can be used to inform on some of the parameter values in my model, I do not have the data necessary to build a very specific model of the growth of resources at rates expected throughout the Pleistocene-Holocene transition[3], or to make

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[3] The NGRIP δ^{18}O dataset can be used as a proxy for temperature during this period, and hence should be correlated with plant growth. However, converting this to an actual value for plant growth rate in the model would involve several assumptions about which unit and scale the value should be in.

quantitative estimates of how farmers/foragers affect their environment. Because of this I chose changes in resource quality to be modelled by simple growth equations which include effects from the foraging/farming efforts of individuals (in a similar way as in Freeman and Anderies (2012) – Equation 2.1).

I will describe and analyse the first version of this model, where only mobility and population size in a foraging population is investigated, in Chapters 4 and 5. This model is referred to as the Forager Model, and warrants a whole chapter of results for at least two reasons: why there might be variation in the mobility of hunter-gathers is still interesting (I dedicated Section 1.4 to this question), and it allows me to understand the workings of the model before adding the extra complexities of subsistence strategy variation.

Before I discuss the development and results of my own model, I will first describe my analysis of the model developed by Bowles and Choi (2013). This is an evolutionary game-theoretical model which looks at the coevolution of farming and farming-friendly property rights, and provided inspiration for the future development of my own model. This chapter is also a case-study of how the FIO method can provide fuller explorations of mathematical and computational models, and how my application of it has revealed new insights into how farming may have developed.

3

Property Rights and Subsistence Strategy Changes

The work in this chapter has been published in:

Gallagher, E. M., Shennan, S. J., and Thomas, M. G. (2015). “Transition to farming more likely for small, conservative groups with property rights, but increased productivity is not essential”. *Proceedings of the National Academy of Sciences*, 112(46):14218–14223.

I quote passages verbatim from this publication and its supplementary material, and all figures have been reprinted with permission. This publication is attached in Appendix N.

Summary

In Chapter 2 I discussed how mathematical models can be used to test theories and explore new hypotheses concerning the origins of agriculture. I examined how evolutionary theory, game theory and agent-based modelling can all be useful in modelling human behaviour. I also saw how models which base their results on ill-defined default parameter values and use a vary-all-but-one method of parameter sensitivity analysis do not provide a complete view of how the model works, are weak in interpretative power and can overlook many interactions between parameters. I proposed the fitting to idealised outcomes (FIO) method in Section 2.4.1 as an alternative method of model exploration and parameter sensitivity analysis.

Bowles and Choi (2013) developed a game-theoretical model for the coevolution of farming and farming-friendly property rights, which replicates the timings for the emergence of these events seen in the archaeological record. Their model was calibrated using the NGRIP climate data (described in Section 2.5.3). Bowles and Choi vary parameters one-by-one to test the robustness of their model, but give little to no indication of where they find the values used in the default parameter set.

In this chapter I replicate the model of Bowles and Choi (2013) and use the FIO method to find complexities and interactions of the model previously unidentified. As I will discuss in Section 7.3 the property rights aspect of Bowles and Choi's model is something I would like to include in a further model at a future date. This chapter also provides an example of implementing the FIO method and by doing so reveals new insights into the origins of agriculture.

In Section 3.1 I will describe the model in full and discuss the results of Bowles and Choi's parameter sensitivity analysis. I will discuss details of my replication of their model and my decisions for certain aspects of the FIO approach in Section 3.2. The results will be given in Section 3.3 and implications given in Section 3.4. Finally I will conclude my findings in Section 3.5.

3.1 The Bowles and Choi Model

It has been argued that during the transition to agriculture, the institution of private property emerged (Bogaard et al., 2009; Earle, 2000; North and Thomas, 1977). This idea led Bowles and Choi (2013) to hypothesise that the advent of farming was impossible without farming-friendly property rights, and vice versa. Furthermore, they posit that farming was not suddenly invented and then adopted because it was a “better way to make a living” (Bowles and Choi, 2013) but, instead, that it was only due to particular rare (and perhaps coincidental) environmental and social conditions that it became established. To study these hypotheses, an agent-based model was developed (henceforth referred to as the Bowles and Choi model), calibrated with a proxy of climate volatility from the North Greenland Ice Core Project (NGRIP) (Andersen et al., 2006; Rasmussen et al., 2006; Svensson et al., 2006; Vinther et al., 2006) – see Section 2.5.3 for details on this. Their simulations show that farming and farming-friendly property rights can coevolve with approximately the same timings and magnitude as indicated in the archaeological record.

3.1.1 Model Details

The Bowles and Choi model (2013) is based on 600 agents (the hypothesised size of a late Pleistocene ethnolinguistic unit), separated into groups of 20 (the size of forager bands or small villages). Agents have two types of strategies: they can be farmers or foragers (their ‘technology strategy’), and they can have a ‘behavioral’ strategy, whereby they can be a sharer, a bourgeois, or a civic (explained later). The model can be split into five sections: within-group interactions, between-group interactions, cultural updating, behavioural experimentation, and migration. All simulations start with a population of civic foragers, representing what may be expected in the late Pleistocene on the basis of generalizations from hunter-gatherer ethnographies (Kaplan et al., 2005).

First, agents obtain their payoffs by foraging or farming. The productivity of foraging, V_h, is normalized to 1, and the productivity of farming is

$$V_a = (r - \theta)z - z, \tag{3.1}$$

where r is the productivity of the farmer’s investment, z is the amount of farming investment, and θ is the disadvantage of farming due to temperature volatility. θ is found by transforming the original NGRIP ice core data to find a value for each 20-y period; details can be found in Bowles and Choi’s supporting information (Bowles and Choi, 2013, SI pg. 17–18). Hence, the value for the productivity of farming changes every 20 y, and iterations of the model are now pegged to specific years. Next, two agents from the same group are randomly paired, and games are played over the distribution of each of the agents' products. The outcomes of these games can increase or decrease the agents' payoffs based on which strategies they both have (see Table 3.1). Key components of this model are the farming-friendly property rights of the bourgeois agents and the 'sharing-enforcer' role played by the civics. A bourgeois agent will never share its own product, it will never contend for a farmed product (the contestability of farming, μ_a, is 0), and it will always try to steal a foraged product (the contestability of foraging, μ_h, is 1). This behaviour is not tolerated by civics, which try to punish the bourgeois individual. Hence, there will be contests between civic foragers and bourgeois agents. The civic wins with a probability, f, increasing with the number of civics in the group:

$$f = \frac{((1-\alpha-\beta)n + 0.5n - \nu)^{\gamma}}{((1-\alpha-\beta)n + 0.5n - \nu)^{\gamma} + (n - (1-\alpha-\beta)n - 0.5n + \nu)^{\gamma}}, \tag{3.2}$$

where n is the size of the group, ν and γ are the centre value and exponent respectively of the winning function – these are set to $\nu = 8$ and $\gamma = 5$ without discussion, and α and β are the proportions of sharers and bourgeois within the group. If the civic wins the product is shared equally between all of the civics in the group, and the bourgeois pays the conflict cost, C. Alternatively, the conflict cost is divided between all of the civics in the group. Thus, these within-group conflicts will not occur if the population consists of either entirely civic or sharer foragers (i.e., the Pleistocene state) or entirely bourgeois farmers (i.e., the Holocene state). Sharers never participate in contests, either sharing or conceding their product depending on whom they interact with.

With a probability of κ, all of the groups are randomly paired and between group contests can occur. The probability a contest occurs between groups i and j is

$$d = \frac{|\pi_i - \pi_j|}{\pi_i + \pi_j} \tag{3.3}$$

where π_i and π_j are the average payoffs of group i and j respectively. The group with the higher average payoff wins with a probability of $0.5 + 0.5d$. Therefore contests are less likely between equally matched groups, and the group with the higher average payoff is more likely to win. Each of the agents in the winning group then gains τ payoff units each, and agents from the losing team lose τ payoff units each.

Next, agents are assigned a cultural model for both strategies. Cultural models are generally chosen from within the same group, with the exception of the loser of a

Table 3.1: Interactions in the Bowles and Choi (2013) model. Outcomes of a game over the row player's product, when the row player is a forager (red) or a farmer (blue). Outcomes that are independent of the row player's technology strategy are shown in black.

	Bourgeois	**Sharer**	**Civic**
Bourgeois forager	Column player will take all row's product with probability 0.5	Row player keeps all of their product	Civics will take all of row's product with probability f
Bourgeois farmer	Row player keeps all of their product		
Sharer forager	Column player will take all of row's product	Row's product will be shared equally	Row's product will be shared equally
Sharer farmer	Row's product will be shared equally		
Civic forager	Column player will take all of row's product with probability (1-f), otherwise row player's product will be shared equally with all the civics in the group	Row's product will be shared equally	Row's product will be shared equally
Civic farmer	Row's product will be shared equally		

between-group interaction, where cultural models are chosen from the winning group. Cultural models are more likely to be from the predominant type of strategy, with the probability that a sharer, bourgeois, or civic is chosen as the cultural model as, respectively, α^η/y, β^η/y, or $(1-\alpha-\beta)^\eta/y$, where

$$y = \alpha^\eta + \beta^\eta + (1-\alpha-\beta)^\eta \tag{3.4}$$

and η is a measure of conformist biased cultural transmission. Figure 3.1 shows how these probabilities can change with η. An agent will copy their cultural model's strategy if it has a higher payoff.

The last stages in the model are behavioural experimentation, where agents will randomly change their strategies with probability ϵ, and migration, where agents migrate from their group with probability m and are randomly assigned to another group.

Bowles and Choi (2013) ran 1,000 simulations of their model over 2,075 iterations (41,500 y) and recorded the percentage of simulations at each iteration that had more than 50% bourgeois farmers. Their results (see Figure 3.2) show a small increase in the number of bourgeois farmers around 15,000-13,000 yBP; this small increase is noted to coincide with short-lived experiments in sedentism and storage seen in the Natufian

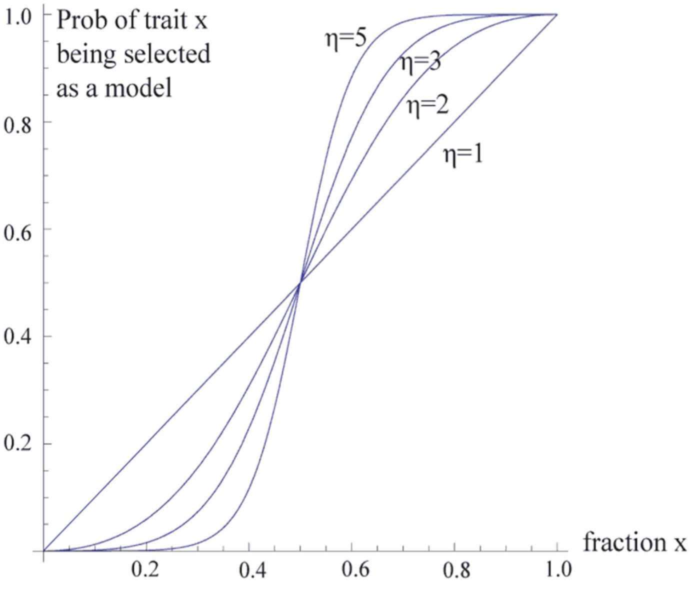


Figure 3.1: How the probability of a cultural model being chosen with a trait of x changes with the fraction of that trait in the population, under different values for η. A reproduction of Figure S3 from Bowles and Choi (2013, SI pg. 11).

culture. After around 11,000 yBP, there is a steady increase in the number of majority bourgeois farmer simulations, fitting with evidence that independent origins occurred after this point in all of the well-studied regions. For any given year, there are always less than 31 of the 1,000 simulations with a bourgeois farmer majority.

The parameters and default values in Bowles and Choi's model are given in Table 3.2.

3.1.2 Parameter Sensitivity Analysis

Bowles and Choi (2013) test the robustness of their model by varying parameters one-by-one, and show that varying parameters through plausible values gives the same outcome as the result with the default parameters, although with changeable magnitudes (Bowles and Choi, 2013, SI pg. 19–23). Figure 3.3 shows their robustness check for the migration rate, where the interpretation would be that increasing the migration rate increases the amount of bourgeois farmer majority simulations. A summary of all Bowles and Choi's robustness checks is shown in Table 3.3.

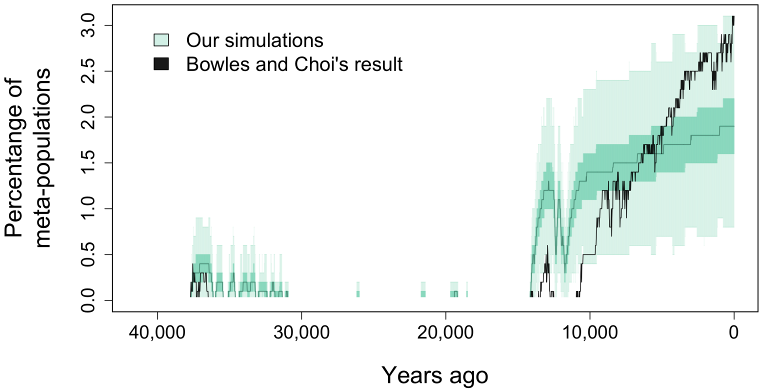


Figure 3.2: Range (light green), interquartile range (middle green), and median (dark green) of the percentage of metapopulations (1,000 simulations) with a majority of bourgeois farmers at each time point when running my interpretation of the model 1,000 times. Bowles and Choi's published result (2013) is reproduced in black.

Table 3.2: Model parameters, their default value used in the Bowles and Choi model, and the range of values sampled from in my FIO analysis if applicable.

Parameter	Symbol	Default value	Range/values
Number of groups	g	30	2, 4, 6, 10, 12, 20, 30, 50, 60, 100, 150, 300
Migration rate	m	0.2	$m \in \mathbb{R} \vert 0 \leq m \leq 1$
Behavioural experimentation	ϵ	0.25	$\epsilon \in \mathbb{R} \vert 0 \leq \epsilon \leq 1$
Cost of losing a conflict	C	1.5	$C \in \mathbb{R} \vert 0 \leq C \leq 10$
Hunter-gatherer product	V_h	1	$V_h \in \mathbb{R} \vert 0 \leq V_h \leq 10$
Contestability of a hunter-gathered product	μ_h	1	$\mu_h \in \mathbb{R} \vert 0 \leq \mu_h \leq 1$
Contestability of a farmed product	μ_a	0	$\mu_a \in \mathbb{R} \vert 0 \leq \mu_a \leq 1$
Resource transfer amount	τ	3	$\tau \in \mathbb{R} \vert 0 \leq \tau \leq 10$
Probability of a between-group conflict	κ	1	$\kappa \in \mathbb{R} \vert 0 \leq \kappa \leq 1$
Farming investment	z	2	$z \in \mathbb{R} \vert 0 \leq z \leq 19.21$
Level of conformism	η	2	$\eta \in \mathbb{R} \vert 0 \leq \eta \leq 5$
Farming product	V_a	$V_a = (r - \theta)z - z$	Not varied
Productivity of the farmers investment	r	1.5	Not varied
Disadvantage of farming due to temperature volatility	θ	$\theta = (0.45 - w)/5$	Not varied
Temperature variability	w	Transformed from raw NGRIP values	Not varied
Centre value of the winning function	ν	8	Not varied
Exponent of the winning function	γ	5	Not varied

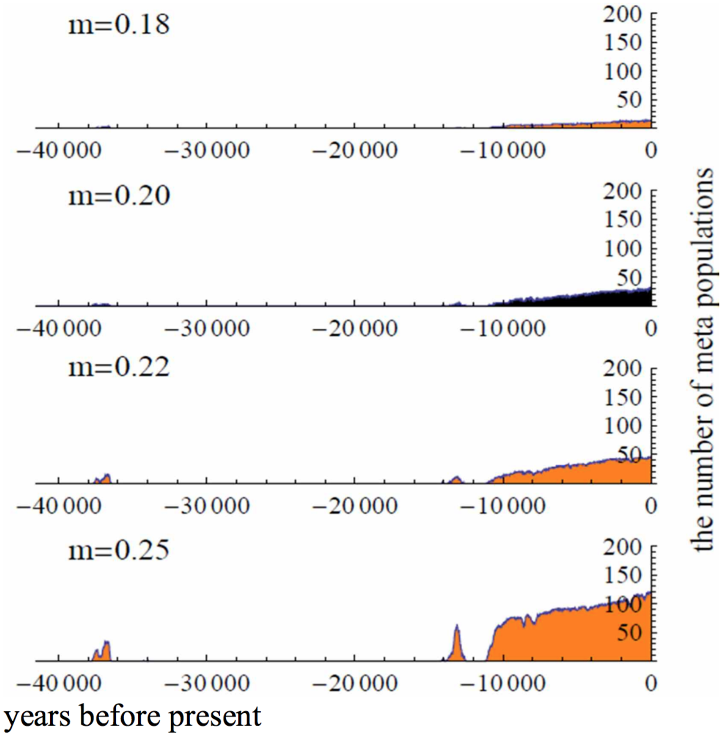


Figure 3.3: An example of one of Bowles and Choi's robustness checks for the migration rate. Taken from Bowles and Choi (2013, SI pg. 21)

Table 3.3: Parameters varied by Bowles and Choi (2013), and the values used. The default values are shown in bold. The result of whether the amount of bourgeois farmer majority simulations increases or decreases when these variations are applied is also noted.

Parameter	Variations	Result
The productivity of the farmers investment, r	1.4, **1.5**, 1.53, 1.57*	Increase**
Migration rate, m	0.18, **0.2**, 0.22, 0.25	Increase
Cost of losing a conflict, C	1.25, **1.5**, 1.75	Increase
Contestability of a hunter-gathered product, μ_h	0.7, 0.8, 0.9, **1**	Decrease
Contestability of a farmed product, μ_a	**0**, 0.05, 0.1, 0.15	Decrease
Resource transfer amount, τ	1, 2, **3**	Decrease
Probability of a between-group conflict, κ	0.33, 0.5, **1**	Decrease
Behavioural experimentation, ϵ	0.24, **0.25**, 0.26	Increase

* r is varied to 1.57 in the Holocene, but kept as 1.5 in the Pleistocene for this change.

** Increase when r is varied through 1.4, 1.5 and 1.53.

3.2 Methods

Using the FIO method, I expanded on the analysis by Bowles and Choi by running the model 1.2×10^7 times with randomly chosen (within defined limits) combinations of parameters (see Table 3.2), selecting the simulations closest to idealized outcomes (the 'top' simulations), and then exploring the patterns and interactions of the parameter values in these top simulations.

In this section I will give details of these processes and the model replication.

3.2.1 Replication

Following some corrections to the published account of the Bowles and Choi model (given in Appendix B) and using some of their code for the within-group interactions, I essentially replicated their published results using the default parameter values. Coding and running information is given in Appendix C.

To look at the variability in my results, I ran the model 10^6 times with the default parameters (given in Table 3.2) and then separated these simulations into 1,000 sets of 1,000 simulations. The range of the number of majority bourgeois farmer simulations at each year for all of these 1,000 simulation sets can be seen in Figure 3.2, along with the published results of Bowles and Choi (which mostly fall into my range). I observed a similar trend to theirs, where the presence or absence of a majority of bourgeois farmers occurs at the same times, and a steady increase in bourgeois farmers also occurs from around 11,000 yBP to the present day. However, because there is no analysis of the variability between different runs of the model in the study by Bowles and Choi (2013), it is not possible to determine whether my results fall into the range of their results.

3.2.2 Parameter Randomization

I varied the following parameters from the Bowles and Choi model (2013): g, V_h, z, μ_h, μ_a, C, κ, τ, η, ϵ, and m. Because the productivity of farming, V_a, changes with both r and z, I elected to vary only z. I kept the overall number of agents in the population at 600, the hypothesised size for an ethnolinguistic group in the late Pleistocene in the study by Bowles and Choi (2013). There are 12 possible values for the number of groups, g, since g needs to be even, divide 600, and result in even-sized groups. The parameters that concern the addition or subtraction from payoffs (C, V_h, and τ) were given a range from 0 to 10 (justified in Appendix D). I made the assumption that the maximum value for V_h is the same as for V_a, because there will be an upper limit to how much a person can benefit from food production. The productivity of farming will be at its maximum when the disadvantage of farming due to temperature volatility (θ) is minimized. Hence, by rearranging the Equation 3.1 for V_a,

$$max(z) = \frac{max(V_a)}{r - \theta_{min} - 1} = \frac{10}{1.5 + 0.0206 - 1} = 19.21. \tag{3.5}$$

The function that defines the probability of a trait being selected for a cultural model converges when η is increased (see Figure 3.1); hence, I only varied η between 0 (no conformity) and 5. The other parameters are probabilities, which I varied through the whole range from 0 to 1. The parameters, their default values, and their range of values varied are shown in Table 3.2.

3.2.3 The Criteria for Ranking

Archaeological evidence indicates that farming in SW Asia had become established by the Late/Final Pre-Pottery Neolithic (9,500 to 8,800 yBP) (e.g., Conolly et al., 2011), hence I ranked the simulations based on the number of farmers they have at 9,000 yBP, where the highest would be classified as the idealized outcome. I show in Appendix E that this number stays roughly the same from 9000 to 0 yBP and that the results would be similar even if I used the number of *bourgeois* farmers at 9000 yBP.

I ran simulations with parameter sets that were randomly chosen from the ranges discussed above. These simulations were then ranked on how close they were to the idealized outcome. Then the next step was to identify trends in the parameter values of the top simulations and correlations between closeness-of-fit rank order and parameter value.

Table 3.4: Statistics from a two-sample Kolmogorov-Smirnov test and a Chi-squared test between the prior (all 1.2×10^7 simulations) and posterior (top 1% of simulations) distributions for each parameter. Only the tests for τ were not significant (p-value ≥ 0.05).

	g	m	ϵ	C	V_h	μ_h	μ_a	τ	κ	V_a	η
D	0.559	0.028	0.781	0.054	0.421	0.008	0.337	0.005	0.031	0.280	0.088
χ^2	159439	489	511448	1833	116176	101	68993	26	613	49264	7453

3.3 Results

Of the 1.2×10^7 simulations run, only ~13% have a majority (> 300) of farmers at 9,000 yBP, and only ~1% of simulations have over 500 farmers (see Figure 3.4). In Figure 3.5 I show the relative frequencies of parameter values when considering the top 1%, 0.5%, and 0.1% of simulations. From this, a simulation's placement in the top 1% of simulations is very sensitive to g, ϵ, V_h, μ_a, and V_a; moderately sensitive to C and η; and relatively insensitive to m, μ_h, τ, and κ (statistics are provided in Table 3.4). Correlation coefficients between the number of farmers and parameter values are shown in Table 3.5. These trends can be clearly seen for the top 1% of simulations in Figure 3.6, and for all of the simulations in Figure 3.7.

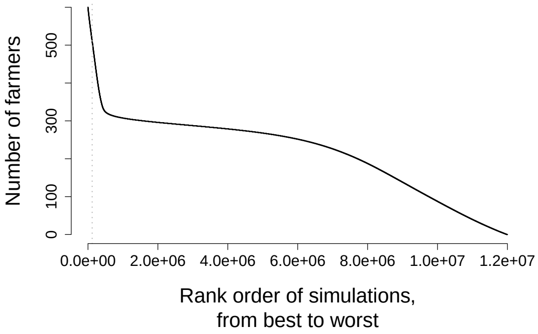


Figure 3.4: The number of farmers in the 9, 000 yBP iteration of each of the 1.2×10^7 simulations. In rank order from the largest (best) to the smallest (worst) number of farmers. The top 1% of simulations are to the left the dashed line.

Parameter interactions, as indicated by correlations between pairs of parameters in the top 1%, 0.5%, and 0.1% of simulations, are shown in Figure 3.8 (coefficients are given in Table 3.6). The largest of these correlations were between g and ϵ ($\rho = -0.402$), V_h and V_a ($\rho = 0.376$), and ϵ and η ($\rho = 0.359$). The relationship between behavioural experimentation (ϵ) and the number farmers for different numbers of groups (g) is shown in Figure 3.9. Here, I see that increasing the amount of behavioural experimentation

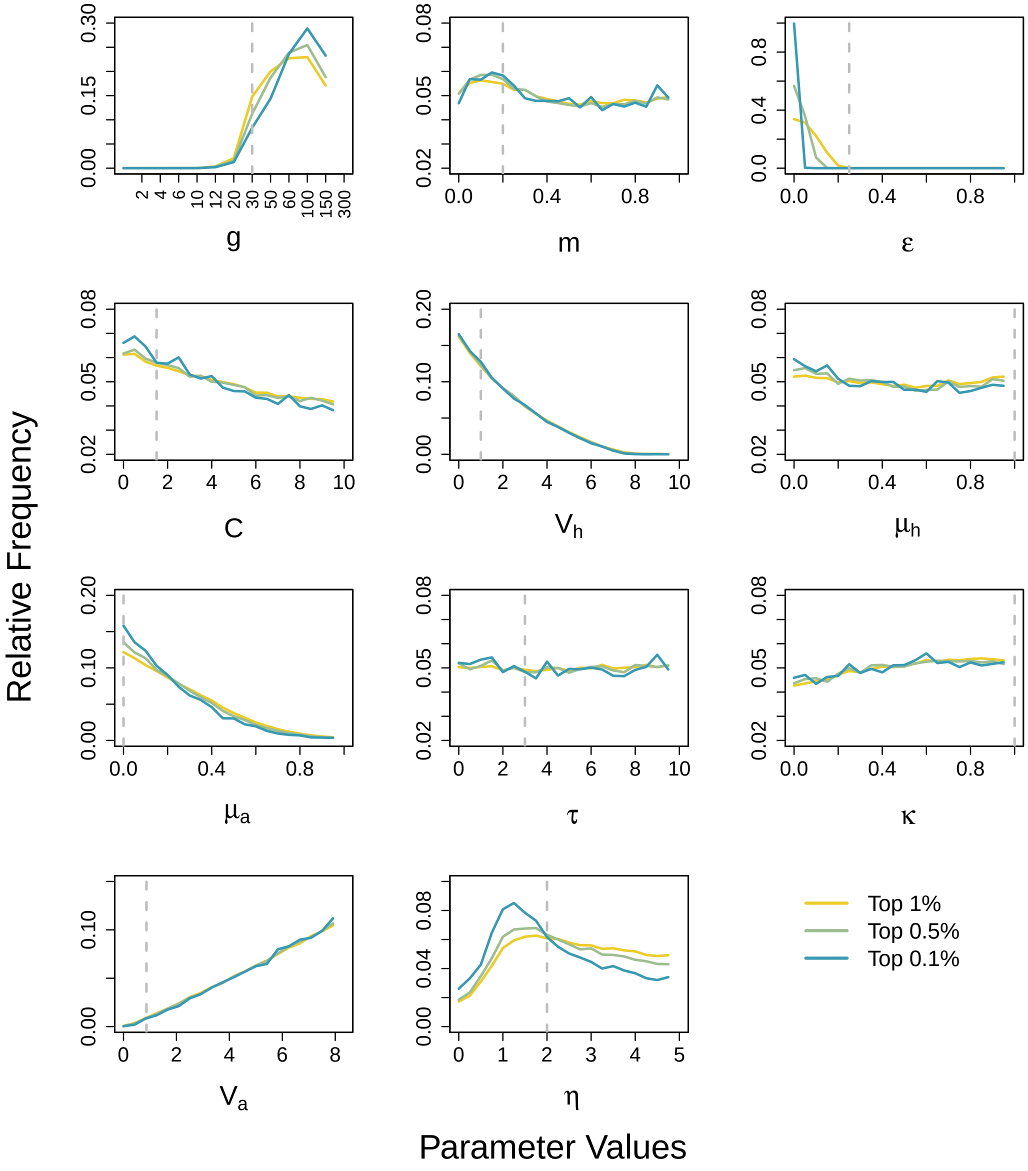


Figure 3.5: Relative frequency plots of parameter values for different top slices of the 1.2×10^7 simulations (top 1% in yellow, top 0.5% in green, and top 0.1% in blue). The vertical dashed lines show the default values chosen by Bowles and Choi (2013). Statistical differences between the distribution of the top 1% of simulations and a uniform distribution for each of the parameters are given in Table 3.4.

Table 3.5: Spearman's rank correlation coefficients, ρ, between parameter values and the number of farmers in different top slices of the 1.2×10^7 simulations. ns – the tests which were not significant (p-value ≥ 0.05).

Simulation fraction	g	m	ϵ	C	V_h	μ_h	μ_a	τ	κ	V_a	η
All	0.31	-0.01	0.72	0.01	-0.20	0.04	-0.07	0.00	-0.00	0.13	-0.11
Top 10%	0.27	-0.01	-0.73	-0.06	-0.26	-0.02	-0.23	0.00^{ns}	0.03	0.19	0.06
Top 1%	0.14	-0.02	-0.74	-0.02	-0.02	-0.03	-0.10	-0.01	-0.02	0.01	-0.11
Top 0.5%	0.11	0.00^{ns}	-0.73	-0.02	-0.01	-0.01	-0.08	-0.00^{ns}	-0.01^{ns}	0.01	-0.11
Top 0.1%	0.05	0.03	-0.65	-0.02^{ns}	-0.02^{ns}	-0.03	-0.01^{ns}	0.02^{ns}	0.00^{ns}	-0.00^{ns}	-0.09

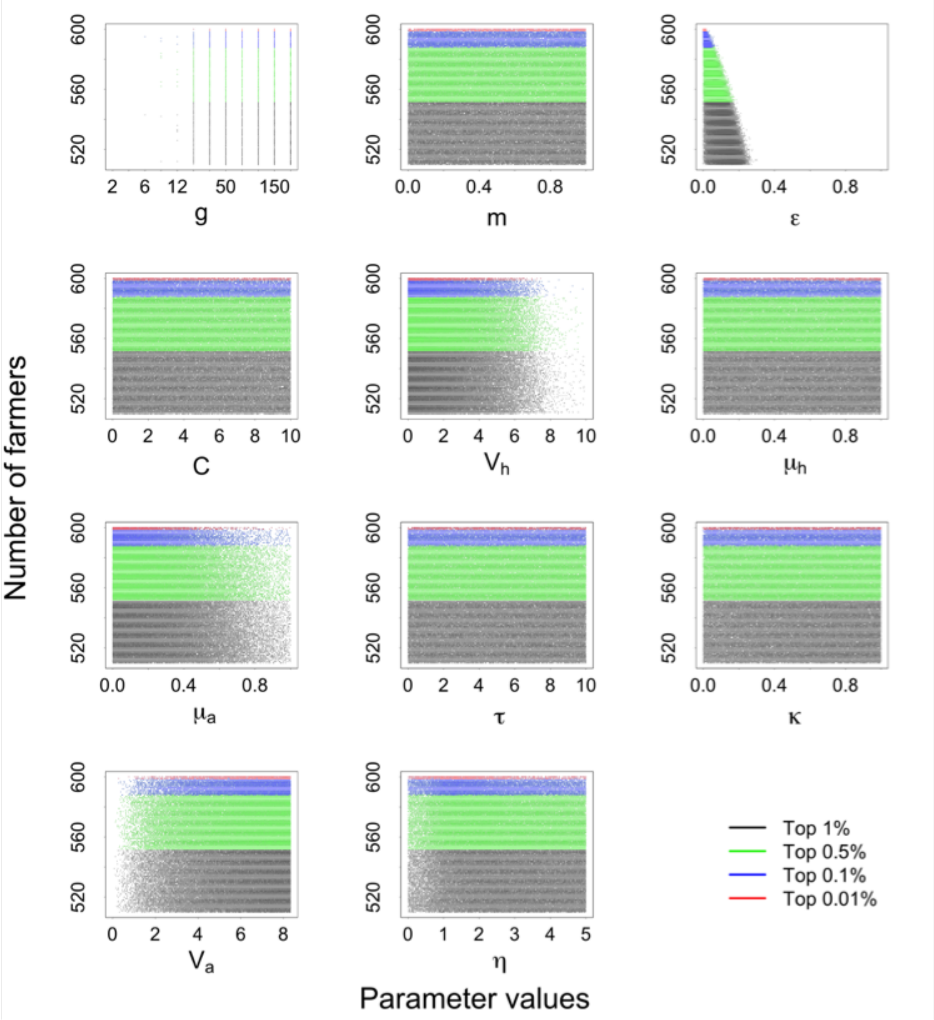


Figure 3.6: The number of farmers and each parameter value for the top 1% (all points), top 0.5% (red, blue and green points), top 0.1% (red and blue points) and top 0.05% (red points) of simulations.

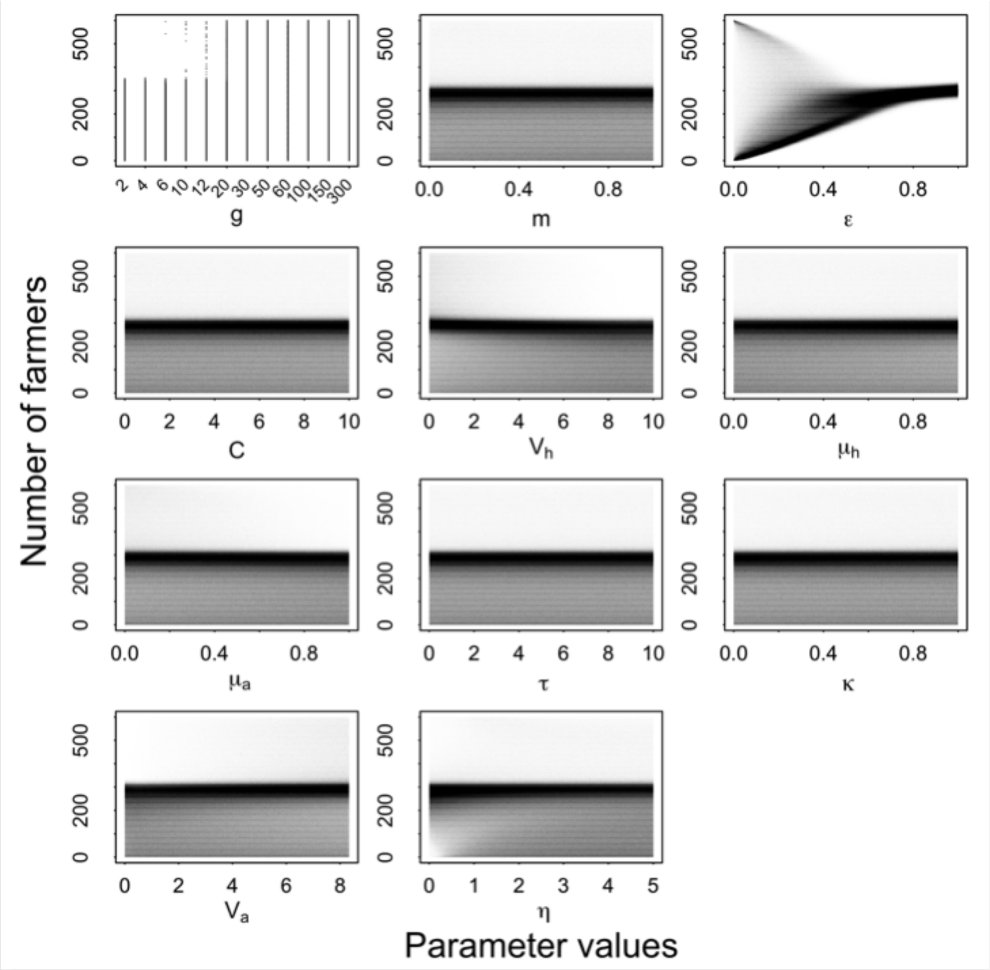


Figure 3.7: The number of farmers and each parameter value for all 1.2×10^7 simulations (each point represents one simulation). Correlation coefficients between parameter values and the number of farmers are given in Table 3.5.

(ϵ) can increase the amount of farming, but the highest numbers of farmers are mostly found in simulations where g is large and behavioural experimentation is low. For the productivities of foraging and farming (V_h and V_a, respectively), I found that in the top 1% of simulations, farming is almost always more productive than foraging (i.e., $V_a/V_h \geq 1$, for 98.1% of these simulations). However, in all simulations (Figure 3.10) there are some (3.66%) with a majority (> 300) of farmers when $V_h > V_a$ holds. The relationship between behavioural experimentation (ϵ) and the level of conformism (η) in the top 1% of simulations is shown in Figure 3.8. It is only for smaller values of η (< 2) that there is a relationship between lowering ϵ and there being a greater number of farmers. I saw little change in the effect of ϵ while increasing η greater than around 2.

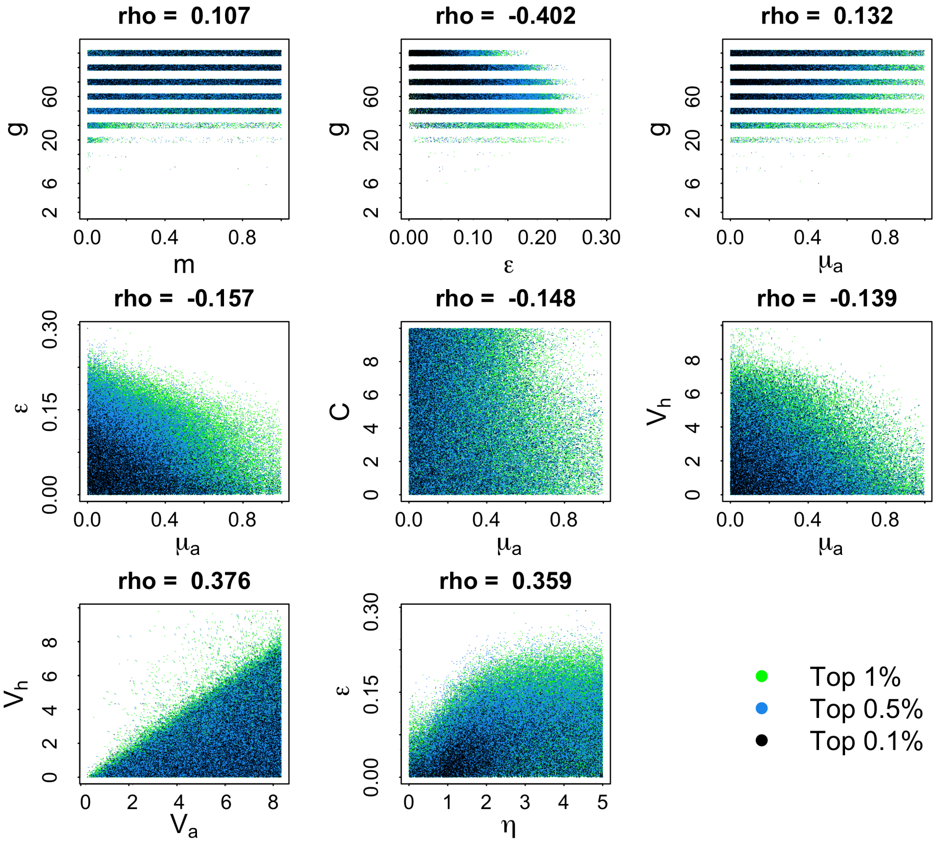


Figure 3.8: Eight significantly (p-value < 0.05) correlated pairs of parameters in the top 1% of the 1.2×10^7 simulations. These plots are broken down into all of the top 1% simulations (green, blue and black points), top 0.5% (blue and black points), and top 0.1% (black points). For ease of interpretation, a small amount of width has been added to the y coordinates of the first three panels, and points plotted randomly within these widths. Spearman's rank correlation coefficient, ρ, is give in the titles.

Table 3.6: Spearman's rank correlation coefficients between all pairs of parameters in the top 1% of the 1.2×10^7 simulations. ns – the tests which were not significant (p-value ≥ 0.05).

	m	ϵ	C	V_h	μ_h	μ_a	τ	κ	V_a	η
g	0.107	-0.402	-0.033	0.063	0.008	0.132	0.006	0.061	0.035	0.044
m		0.021	0.015	0.025	-0.006^{ns}	-0.031	0.003^{ns}	-0.004^{ns}	-0.012	-0.034
ϵ			0.009	-0.056	0.007	-0.157	0.012	0.030	0.001^{ns}	0.359
C				0.031	-0.002^{ns}	-0.148	-0.005^{ns}	-0.003^{ns}	0.006	-0.020
V_h					0.023	-0.139	-0.002^{ns}	-0.002^{ns}	0.376	-0.015
μ_h						0.004^{ns}	0.004^{ns}	0.021	-0.013^{ns}	-0.021
μ_a							0.008	0.053	0.063	0.001^{ns}
τ								-0.005^{ns}	0.001	0.002^{ns}
κ									0.005	-0.011
V_a										0.012

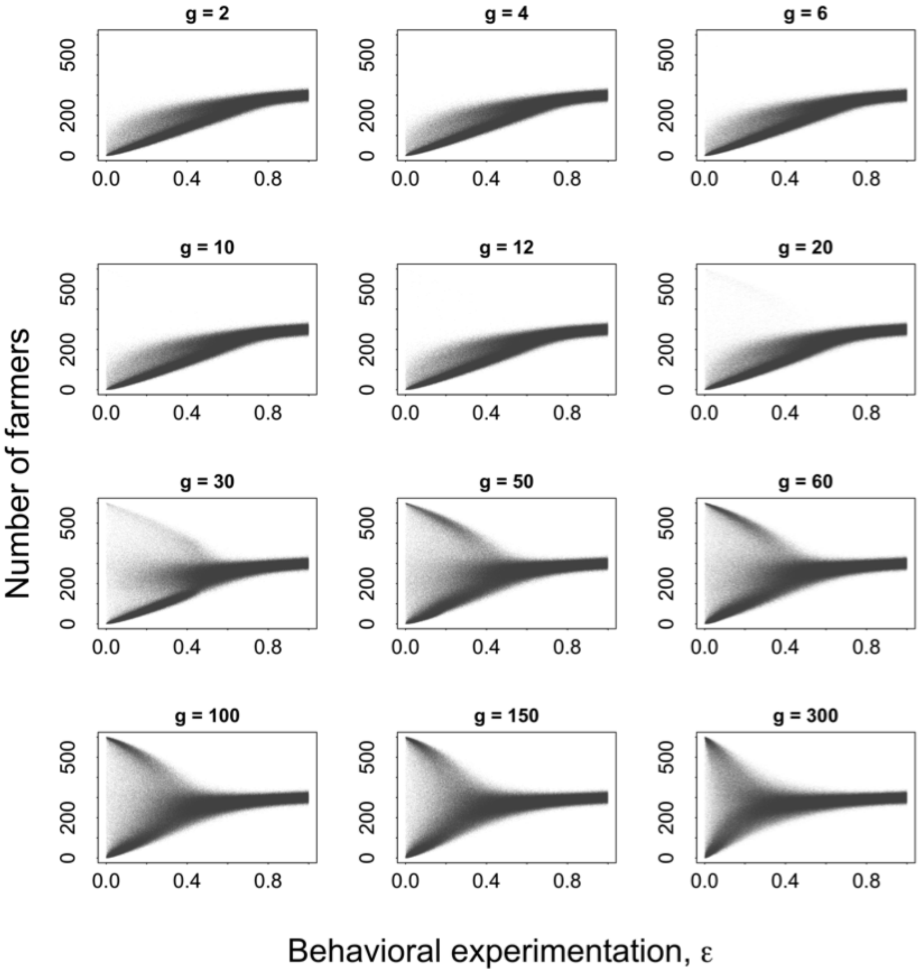


Figure 3.9: Relationship between behavioural experimentation (ϵ) and the number of farmers for simulations with different numbers of groups (g), using all 1.2×10^7 simulations (each point represents one simulation).

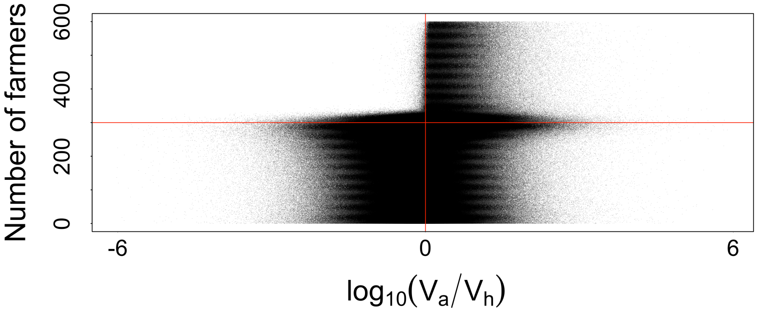


Figure 3.10: Ratio of farming productivity to foraging productivity (V_a/V_h) and the number of farmers in all 1.2×10^7 simulations; a $log_{10}(V_a/V_h)$ scale is used. The vertical red line shows when the ratio is 1 (i.e., $V_a = V_h$), and the horizontal red line shows the boundary between majority farming and majority foraging simulations. Hence, there are some simulations with a majority of farmers when $V_a < V_h$ (top left quadrant).

3.4 Discussion

My analysis has highlighted that the parameters g, ϵ, V_h, μ_a, and V_a (or z) are the most influential parameters on the number of farmers at 9,000 yBP in the model. Therefore, I suggest that group structuring, behavioural experimentation, property rights, and the ratio of farming productivity to foraging are most important for the emergence of farming using this model. I will explain these in more detail in this section.

3.4.1 Structuring

This work has highlighted the relationship between the number of groups (g) and the amount of behavioural experimentation (ϵ) (Figure 3.9). By increasing ϵ, I see an increase in the number of farmers. However, this increase converges to around 50% farmers, because when ϵ is large, agents are changing regularly between both strategies and there is little structuring in the group. It is only when the number of groups is large (i.e., the groups are small) that there starts to be more simulations that have a majority of farmers. Because the simulations all started with a civic forager population, it could be that a single farmer in a large group would be more at a disadvantage than it would in a smaller group, and hence farming would be less likely to emerge as a majority. In fact, it is increasingly unlikely that a bourgeois will win a civic-bourgeois contest in a civic majority group when groups are large (see Figure 3.11). When groups are smaller, I also see that there are more majority farmer simulations as the behavioural experimentation decreases; possibly because high values for ϵ disrupt any structuring, resulting in property rights and farming failing to coevolve. Hence, I predict that farming should emerge when there is low behavioural experimentation and groups are as small as possible (groups smaller than around four or six members are ethnographically improbable anyway). Interestingly, this prediction is consistent with some models of the emergence of prosocial behaviour, whereby cooperation (of which farming property rights are an example) is unlikely to emerge in large groups (Barcelo and Capraro, 2015; Boyd et al., 2014; Nosenzo et al., 2015; Powers and Watson, 2011).

3.4.2 Conservatism

Another finding of this work is that to generate large numbers of farmers or foragers, behavioural experimentation (ϵ) should be low (Figure 3.5). Because the model starts with all foragers, to generate farming, ϵ must not equal 0. However, as behavioural experimentation approaches 1, there will be equal numbers of foragers and farmers,

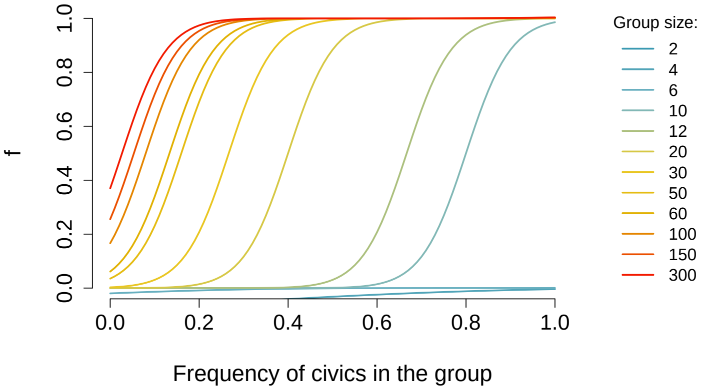


Figure 3.11: The probability of a civic winning a bourgeois-civic interaction, f, when group size and frequency of civics are varied.

because people will be constantly switching from one to the other as explained above. Hence, I predict that conservatism (defined as a low rate of switching between strategies) helps the emergence of farming, and so long as farming is introduced into the population, it will be selected for.

3.4.3 Property Rights

This analysis lends further support to the conclusion by Bowles and Choi (2013) that farming and farming-friendly property rights can coevolve. One illustration of this support is that although there could be no property rights (which was when farming property is always contested, $\mu_a = 1$), I still saw a greater proportion of farmers as the contestability of a farmed product (μ_a) approached 0 (Figure 3.5). Conversely, I also found that varying degrees of property rights for foraged products, μ_h, had little influence on the number of foragers (as seen by the absence of any trend in the μ_h panels of Figure 3.5, 3.6 and 3.7, and by the low correlation coefficients in Table 3.5. Furthermore, the relationship between μ_a and the number of farmers appears similar to one of exponential decay as the size of the top slice is decreased (Figure 3.5). This trend would be expected if farming-friendly property rights were a main cause of farming in the model.

3.4.4 Ratio of the Productivity of Farming to Foraging

The results also showed that the productivity-of-farming to productivity-of-foraging ratio (V_a/V_h) has an important effect on farming, where $V_a > V_h$ almost always holds in the top 1% of simulations. However, there are some simulations with a majority of farmers where $V_a < V_h$ (Figure 3.10). Thus, there are cases where farming emerges despite the productivity of foraging being greater than the productivity of farming. This observation lends some support to the result of Bowles' study (Bowles, 2011), where it was found that the productivity of farming did not need to be greater than the productivity of foraging for early farmers.

3.4.5 Cost of Conflict and the Level of Conformity

The proportion of farmers at 9,000 yBP was moderately sensitive to parameters C and η, the cost of conflict and the level of conformity, respectively. The frequency decrease as the cost of conflict is increased (Figure 3.5) may be because this change has the most impact on bourgeois agents, as civic foragers share the cost. Because I saw that the amount of farming is increased by farming-friendly property rights, fewer bourgeois agents would mean fewer farmer agents. Thus, costly conflicts result in less farming in this model. For η, the level of conformity, the highest frequency value in the top simulations approaches around $\eta = 1$ as the top slice gets smaller (Figure 3.5). This result may be because as η increases, if a strategy's frequency is below 0.5 in the group, it is increasingly unlikely that this strategy will be a cultural model for another agent (Figure 3.1); thus, this strategy may have little chance of propagating in the population. Hence, for a farming strategy (which starts from a frequency of 0) to become the main strategy in a population, η cannot be too large. On the other hand, at $\eta = 0$ (no conformity), the probability that a farmer or a forager agent will be selected as a cultural model is always 0.5 independent of frequencies in the group; therefore, I see most simulations leading to a near 1:1 farmer/forager ratio (Figure 3.7). Thus, for farming to do well in this model, there should be low (but nonzero) levels of conformity.

3.4.6 Insensitive Parameters

There were a number of parameters whose values were relatively unimportant for the emergence of farming in the model. These parameters were the migration rate (m), the contestability of a foraged product (μ_h; discussed earlier), the resource transfer amount (τ), and the probability of a between-group conflict (κ). Because varying κ and τ will affect agents' payoffs and the spread of farming or foraging equally, it might be expected that these parameters would not make a difference to the amount of farming. Thus, the likelihood and intensity (in terms of potential payoff losses and gains) of between-group conflicts are not driving forces in the emergence of farming in this model. If there was any intergroup violence associated with the Neolithic transition (although there is little evidence for it; Ferguson, 2013), this analysis suggests it was caused by the transition, rather than causal of the transition.

The probability of migration between groups also makes little difference to the emergence of farming. Perhaps in this model, intergroup cultural updating drives the mixing of different strategies in the population, and so migration among well-mixed groups will not introduce new strategies into groups.

3.4.7 Assumptions and Caveats

As with all models, there are many assumptions and simplifications in the Bowles and Choi model (2013). For example, would cultural updating be likely to occur for every agent at each iteration, would an individual's technology be as binary as 'farmer' or 'forager', and is it likely that foraging and farming productivity are independent of one another?

Whereas the Bowles and Choi model (2013) and the analyses here are primarily concerned with the initial establishment of farming groups, other factors are likely to have influenced farming's growth, sustainability, geographical spread, and archaeological visibility. These factors include the availability of suitable plant and animal species for domestication, other local climate and ecological factors, and technological innovations, all of which are likely to affect the relative productivity of farming to foraging (V_a/V_h). In addition, it is likely that farming activity itself changes V_a/V_h, to varying extents in different regions, as a niche construction process (O'Brien and Laland, 2012).

An issue with this approach is making sure that enough simulations were collected, because insufficient simulations can result in poor assessment of model behaviour. However, because the relative frequency plots in Figure 3.5 do not change greatly with more narrow top slices, I am confident that running more simulations would have only smoothed these plots, rather than supporting different interpretations. Because this approach does not fit to empirical data, there could be another issue in finding what the 'idealized outcome' should be. If there are multiple possibilities, as many as possible should be tested. In the case of this work, I found that using various other possible idealized outcomes (number of bourgeois farmers at 9,000 yBP, number of farmers at 0 yBP, and minimum and average number of farmers between 0 and 9,000 yBP) made very little difference to the overall results (shown in Figure E1 of Appendix E). Furthermore, it is important to pick parameters from a sensible range of values. If the range covers unrealistic values, there will be unnecessary simulations; on the other hand, if the range does not cover all of the realistic values, there could be unseen trends. This work erred on the side of caution; most of the parameter ranges cover all plausible values (parameter ranges are justified in Section 3.2.2 and Appendix D).

3.5 Conclusion

In this chapter I have replicated the results of the Bowles and Choi model (2013) and implemented the FIO method to explore the parameter space and parameter interactions of this model. To my knowledge, this is the first use of this approach in archaeological modelling.

This analysis also allowed me to hypothesise that a number of elements are key for the emergence of farming. These elements are as follows: a population structured into groups, small (but not too small) group sizes, a very low amount of behavioural experimentation, and the presence of farming-friendly property rights. I also found that although it is beneficial for farming when its productivity is greater than the productivity of foraging, it is not essential for its emergence; this result is consistent with previous findings (Bowles, 2011). Additionally, the results indicate that costly conflicts within the groups, and high levels of conformity when groups are culturally updating, result in less farming. Furthermore, I found that migration rate and the likelihood and intensity of between-group conflicts are unimportant for the emergence of farming in this model.

To an extent, these analyses contradict the robustness checks reported by Bowles and Choi (2013) and reveal parameter complexities and interactions previously unrecognized. They have also allowed me to examine the effects of simultaneously varying parameters, which was not possible using the fix-all-but-one parameter approach. In comparison to Bowles and Choi's robustness checks (summarized in Table 3.3), the small range of variations in m led to an increase in farming using 1,000 simulations in Bowles and Choi's study (2013), but I saw no overall effect when looking at the full range of m in over 103 times as many simulations. Similarly, when Bowles and Choi (2013) increased the contestability of a foraged product (μ_h), the resource transfer amount (τ), and the probability of a between-group conflict (κ), they found a decrease in the amount of farming, whereas I found no significant differences. Furthermore, they found an increase in the amount of farming when increasing either the cost of conflict (C) or behavioural experimentation (ϵ), whereas I found a decrease in both cases. However, for an increase in the contestability of a farmed product (μ_a), we both predicted that there will be a decrease in the amount of farming.

The findings from this analysis highlight key conditions for the origins of agriculture, which could be investigated in more detail in future studies (e.g., asking whether groups were small during the transition to agriculture). This work also highlights the problems of the fix-all-but-one parameter approach, and serves as an example of this type of parameter analysis in the field of computational modelling in archaeology as a means of exploring past processes.

Bowles and Choi's model was developed to look at the role of property rights in the evolution of farming. Their main finding was that farming-friendly property rights and farming co-evolved when they did. Bowles and Choi's predictions of the increase in Bourgeois farmers almost exactly mirrors climate stabilisation (as measured by the NGRIP data). Teamed with the fact that little reasoning is given to how the NGRIP data is transformed to calibrate farming productivity in the paper, I am not sure how much the model should be praised for replicating the timings of the origins of agriculture. I do think the results hold theoretically though, and the role of climate amelioration can be said to encourage farming.

In the Bowles and Choi model there is a fixed population size and migration is concerned with strategy mixing, rather than having any effect on productivity. Bowles and Choi take as given the 'sedentary nature' of farming, and imply that only after farming was established would population increases be seen. Having seen in Section 1 that there is some evidence that sedentism could come before farming and that it is unclear whether population pressure may have been a contributing factor in the switch to farming, I think Bowles and Choi's assumptions are perhaps too generalised.

In the next three chapters I will develop my own models for mobility decisions and the origins of agriculture. In the further work section of Chapter 7 I will discuss how I could include elements of Bowles and Choi's model into my own.

4

The Forager Model

Summary

In Chapter 1 I discussed the multitude of factors and influences surrounding the origins of agriculture, and how the impacts and dynamics of some of these are still not fully understood. I showed how the transition to farming involved several other behavioural changes, and in Chapter 2 showed how evolutionary theory and mathematical modelling can be used to understand these behaviour changes. The work reviewed in these chapters has provided the motivation to create a new agent-based evolutionary model to specifically look at how mobility, population density and human-environmental interactions are interlinked with the origins of agriculture. This cultural evolutionary model will be influenced by the existing models reviewed in Section 2.3.

In this chapter I will introduce the first stage of my model's development which only considers a foraging population. I will refer to this model as *the Forager Model*. The Forager Model is analysed and discussed in Chapter 5, and in Chapter 6 the addition of allowing agents to forage and/or farm is added. The purpose of considering the model with and without the possibility of farming is both because it is easier to understand the workings of the model before adding more complexity, and also since it is still worth exploring the relationship between mobility, population size and environmental impacts in hunter-gatherers (which was looked at Section 1.4).

This chapter will thoroughly explain the specifics of the Forager Model. Details about the sites are given in Section 4.1, agent qualities are discussed in Section 4.2, agent fission is explained in Section 4.3, strategy mutation in Section 4.4, agent movement in Section 4.5, and details of model initialisation and iterations are given in Section 4.6. A diagrammatic overview of the Forager Model is given on page 144.

Model Overview

The Forager Model simulates **families** moving around a **region** over many years. The model is iterative and each iteration is one year. The region is split up into **sites** of the same size, and each of these sites has a dynamic **foraging quality**. Foraging quality can be thought of as the potential for foraging or, equally, the quality of the natural resources. Foraging resources stay within each site, and in this way do not include migrating animals. Family units (or 'agents') occupy one site each iteration (although many families can co-occupy a single site), and forage at this site. The family's foraging creates a feedback between the foraging quality of the site and the family's **fitness**. Families can die, **fission**, **mutate**, and **move** from site to site, according to different probabilities. A visualisation of two iterations of the model can be seen in Figure 4.1 and the stages of the model are shown in the flow diagram on page 131.

These dynamics will be explained in more detail in the sections to come. For good practice, I also explain the model using the ODD protocol (Grimm et al., 2010) in Appendix F.

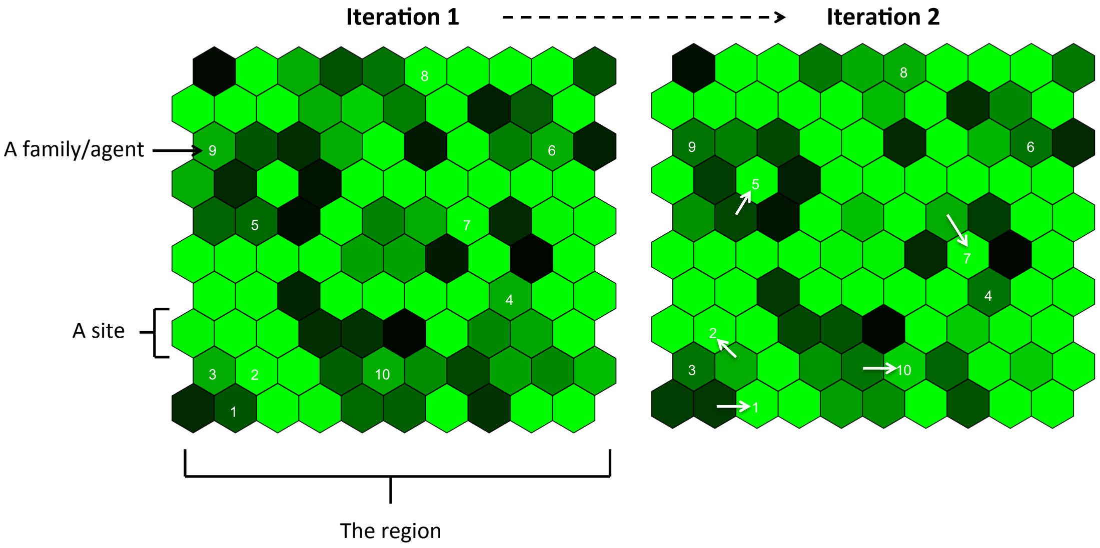
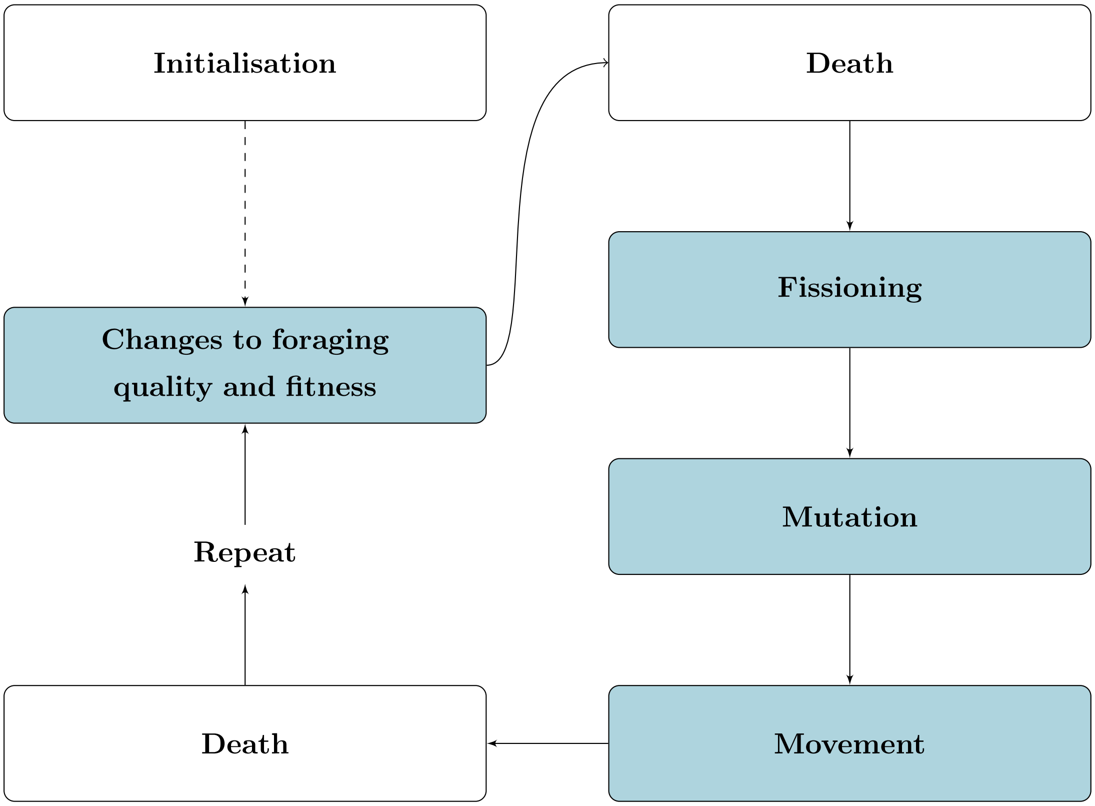


Figure 4.1: Visualisation of the model. Agents (white numbers) move from site to site (green hexagonals). The shade of the hexagonal reflects the foraging quality of the site – where the best quality is shown in bright green, and worst quality in dark green. The foraging qualities change from year to year according to natural growth and depletion.



4.1 Sites

The region modelled is made up of a hexagonal grid of sites with s_x sites in the horizontal direction and s_y in the vertical direction. The hexagons are regular and so each of their sides has the same length. The sites have coordinates found by using a 3D coordinate system – illustrated in Figure 4.2.

At each iteration sites have a foraging quality value and can be occupied by agents or left unoccupied.

4.1.1 Foraging Quality

I assume there are two forces which act on the dynamics of a site's foraging quality, q_f; natural growth, and depletion when agents forage at the site.

Similarly to Marceau and Myers (2006) and Freeman and Anderies (2012) I assume foraging quality grows according to logistic growth with a carrying capacity of 1 and a growth rate of r. I also assume that the amount of depletion is density dependent. Thus

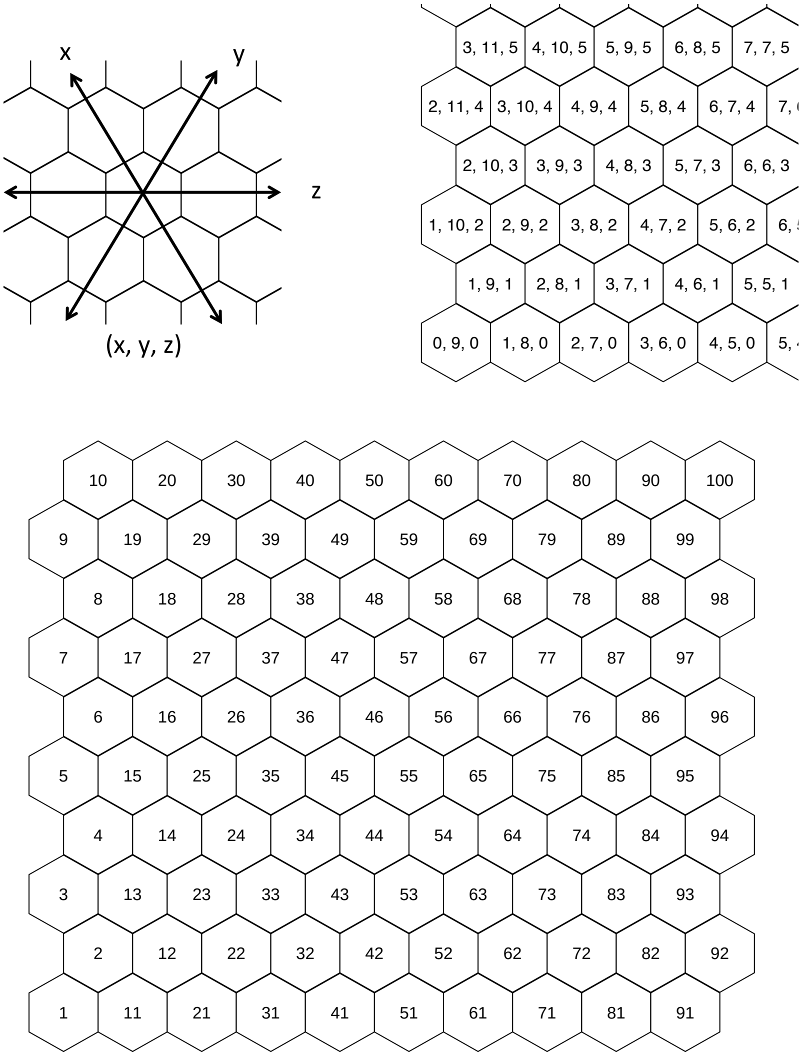


Figure 4.2: Coordinate system used for sites (above) and the indexes used (below).

at iteration $t + 1$ the foraging quality at a site is

$$q_{f,t+1} = q_{f,t} + rq_{f,t}(1 - \frac{q_{f,t}}{1}) - \lambda(1 - \frac{1}{n+1})q_{f,t}, \tag{4.1}$$

where n is the number of agents which occupy this site and λ is the depletion scalar. Thus when the site is unoccupied there is no depletion effect ($1 - \frac{1}{n+1} = 0$) and when the site is occupied the depletion impact is logarithmically increasing with the number of agents – shown in Figure 4.3. The dynamics of how the foraging quality varies over time for different values of r and λ, but when the number of agents stays at 1, are shown in Figure 4.4.

In this model $q_f \in [\, q_{f,min}, 1]$, where $q_{f,min} > 0$. I do not allow the foraging quality to reach 0 since if it did it could never grow back (see Equation 4.1).

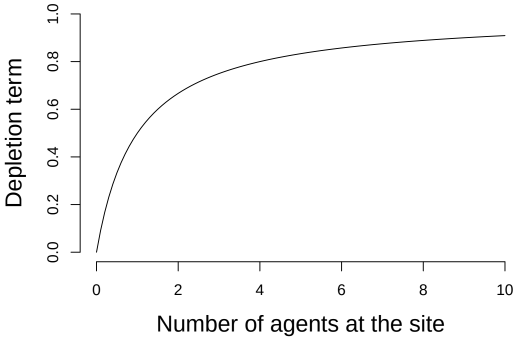


Figure 4.3: The effect the number of agents has on the depletion term, $1 - \frac{1}{n+1}$.

4.2 Agent Movement and Fitness

Agents have a mobility strategy which determines how likely they are to move site every iteration, m. Thus every iteration an agent moves site with a probability of m. An agent's mobility strategy can mutate and I set $m \in [\, 0.01, 0.99]$ – explained in Section 4.4. I refer to agents being sedentary if their mobility strategy is close to 0, and highly mobile if their strategy is close to 1.

Agents also have a fitness[1] measure, $f \in [\, f_{min}, 1]$, which changes within the lifetime of the agent. If $f < f_{min}$ then the agent dies. An agent's fitness at iteration t is calculated as

$$f = q_{f,t-1}/n, \tag{4.2}$$

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[1] Although related, I use the term 'fitness' to refer to well-being rather than fecundity.

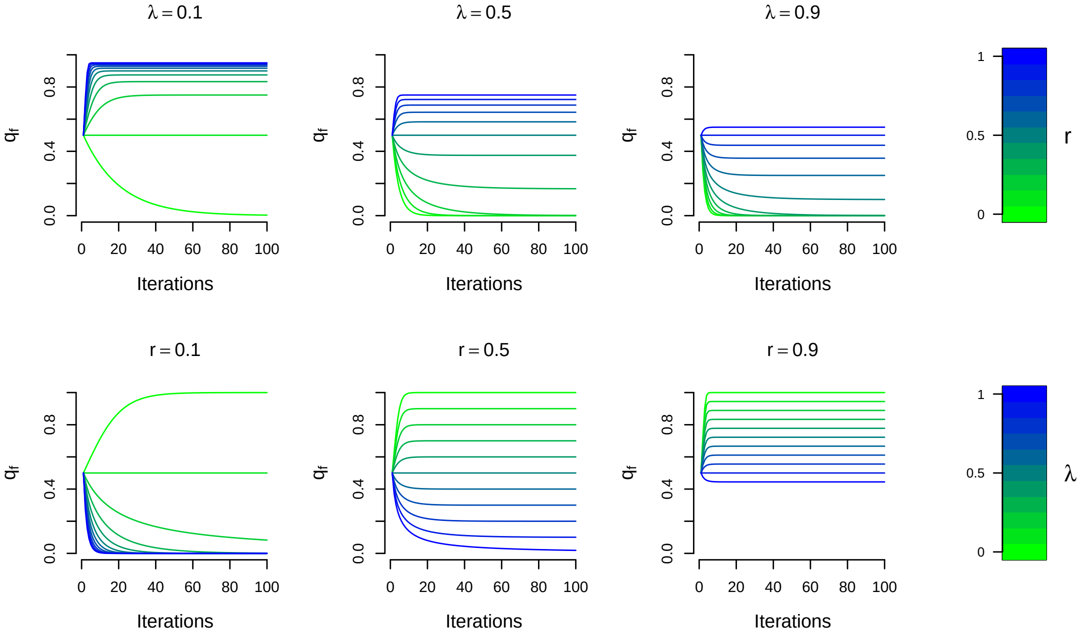


Figure 4.4: How the foraging quality changes over time when the site is always occupied by one agent. I vary the value of r and set λ to 3 different values (top row) and I vary λ and set r to 3 different values on the bottom row.

where $q_{f,t-1}$ is the foraging quality (in the previous iteration) of the site the agent occupies, and n is the number of agents which occupy this site. Hence, there is no accumulation of fitness as the agent's fitness in the last iteration does not affect its current fitness.

Using Equation 4.2 the maximum number of agents that can survive at a site, n_{max}, is :

$$n_{max} = max(n) = max(\frac{q_{f,t-1}}{f}) = \frac{max(q_{f,t-1})}{min(f)} = \frac{1}{f_{min}}, \tag{4.3}$$

and therefore $f_{min} = 1/n_{max}$.

4.3 Family Fission

The agents in my model are families, and as long as their fitness is never below f_{min} they have the potential to exist indefinitely in the model. The model assumes new generations replace the older generations, and incest is avoided by mixing amongst different families (for example the young female members of two families swapping). I have chosen not to model these or other population dynamics (for example birth and death of individual people within the family) since these are individual dynamics and add an unnecessary level of detail.

A successful family could be interpreted as one which is able to support a large number of members, and hence a high fitness could mean that a family has a higher chance of being able to split into another family. Therefore, new families occur not because of birth, but because the 'parent' family was fit enough to fission into a new one.

When fission happens the new family occupies the same site as the parent family, but it is free to move site in the next iteration. The new family will have the same strategies as its parent and a randomly chosen initial fitness value.

4.3.1 Probability of Fission

Thus, there is a need for a function which describes the relationship between a family's fitness and its probability of fissioning, p. I set it so that if an agent has the minimum agent fitness (f_{min}) then there is a 0 chance of fissioning. Finding the upper probability of fitness is slightly tricky, since it is not realistic that full fitness would mean there was 100% chance of fissioning every iteration.

Based on the work by Mace (1996) (discussed in Section 2.5.1) the relationship between wealth and fertility can be modelled as

$$\text{fertility} = c + d\log(\text{wealth}), \tag{4.4}$$

where the c and d are constants. This is shown in Figure 4.5a. I will use this relationship between my agent fitness (which can be thought of as a measure of wealth) and fission probability (which should be proportional to fertility). Hence I take,

$$p = c + d\log(f). \tag{4.5}$$

The upper limit for the probability of fission, p_{max}, will be reached when agent fitness is 1. Hence $p_{max} = c + d\log(1)$, and thus

$$c = p_{max}. \tag{4.6}$$

Since the probability of fission is 0 when fitness is at its minimum, f_{min}, then using Equations 4.5 and 4.6 I can find d,

$$0 = p_{max} + d\log(f_{min}) \Rightarrow d = \frac{-p_{max}}{\log(f_{min})}. \tag{4.7}$$

Thus substituting equations (4.7) and (4.6) into (4.5) I have

$$p = p_{max} - \frac{p_{max}}{\log(f_{min})}\log(f) \tag{4.8}$$

where $p_{max} \in [0, 1]$.

I can find a estimated value for p_{max} by using the data on hunter-gather fertility and mortality from Kelly (2013) which was summarised in Table 2.6 in Section 2.5.1. Using this the average fertility rate of the sample of hunter-gatherer groups is 5.7, with a minimum of 2.6 and a maximum of 8.5, and the average mortality for children < 15 years old was 35.3%.

Assuming that children under 15 are not reproductive, then using the average childhood mortality, the proportion of children who survive to reproductive age is

$$1 - \frac{35.3}{100} = 0.647. \tag{4.9}$$

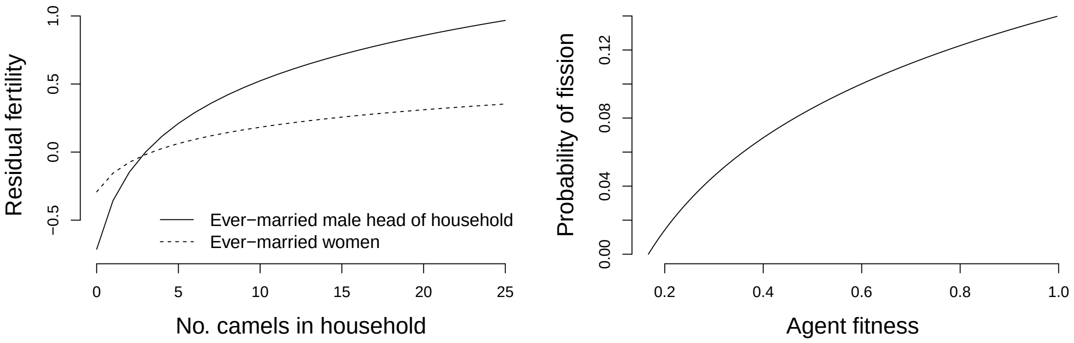
And thus the number of children a woman will have that survive to a reproductive age is the proportion who survive to reproductive age multiplied by the total fertility rate. From the ethnographic data this is a minimum of $0.647 \times 2.6 = 1.68$ children and a maximum of $0.647 \times 8.5 = 5.50$ children (using the minimum and maximum total fertility rates respectively).

For the family units in my model (the agents), I assume that two children need to stay in the family to replace the previous generation, but any other children can form new families. Therefore I find the family fission probability every year should be

$$\frac{\text{Number that survive to a reproductive age} - 2}{\text{Generation time}}. \tag{4.10}$$

If we set the generation time, G, to 25, then the lower fission probability is $\frac{1.68-2}{25} = -0.0128$ (in effect this is 0), and the upper fission probability, p_{max}, is $\frac{5.5-2}{25} = 0.14$.

The modelled relationship between fitness and fission probability using $p_{max} = 0.14$ can be seen in Figure 4.5b. The number of years until there is a new family based on these fission probabilities is simply $1/p$.



(a) **(b)**

Figure 4.5: The relationship between wealth and fertility. (a) The best fit regression curves of data on the number of camels in the household (a measure of wealth) and the residual fertility of ever-married male head of household (solid line) and ever-married females (dashed line), from a study by Mace (1996) on 848 Gabbra households. Reproduced from Mace (1996). (b) My modelled relationship between fitness and probability of fission (Equation 4.8) using $f_{min} = 1/6$ and $p_{max} = 0.14$ based on Mace (1996) and ethnographic data from Kelly (2013).

4.4 Mutation

With a probability of $\mu \in [0, 1]$ each iteration and for all agents, an agent will mutate its mobility strategy. This mutation could be thought of as random experimentation or cultural learning. I will assume that approximately every generation, which I take as 25 years, a family changes the way it moves, and thus $\mu = 1/25 = 0.04$.

I use a Binomial distribution to pick the new mutated strategy value from, where the distribution is influenced by the agent's original strategy value, m_0, and fitness, f:

$$B(n^*, p^*) = B(\kappa_m f, m_0) \tag{4.11}$$

where the parameter κ_m is a measure of mobility strategy conservatism. This distribution means that the strategy value will not change much if the agent is successful, and conversely if the agent is not very fit then the agent will be less conservative. Values chosen from this distribution then need to be divided by $\kappa_m f$ so that the agent's new mobility strategy is between 0 and 1. Figure 4.6 shows the distributions the new strategies would be picked from under a few different circumstances.

Using a Binomial distribution also makes sense as a model for cultural transmission, since the value for the number of components in the distribution can be thought of as the number of components that make up mobility. However, there is the problem that when the agent's strategy is 0 or 1 then the variance is 0 (variance $= n^*p^*(1 - p^*)$). Thus there could be fixation to only either mobility strategies of 0 or 1 if these values ever occur. Hence, to avoid this issue I pick the strategies from between $[0.01, 0.99]$. If a strategy value of < 0.01 or > 0.99 is selected then it is set to 0.01 or 0.99 respectively.

4.4.1 Selection and the Null Strategy

The model allows for the evolution of the mobility strategy. For example, if high mobility results in higher agent fitness than low mobility does, then agents with low values for m will be more likely to die, and agents with high values for m will be more likely to live and fission (where they pass on their high m value). This means that high m values will persist in the population. Furthermore, I introduce variation into the population via the mutation step, so new, possibly more advantageous, strategy values enter the population.

Thus I can see whether there are any circumstances which cause a selection pressure for certain mobility strategies. This could be seen by a change in the frequencies of strategy values in the population over time. However, such changes could also occur

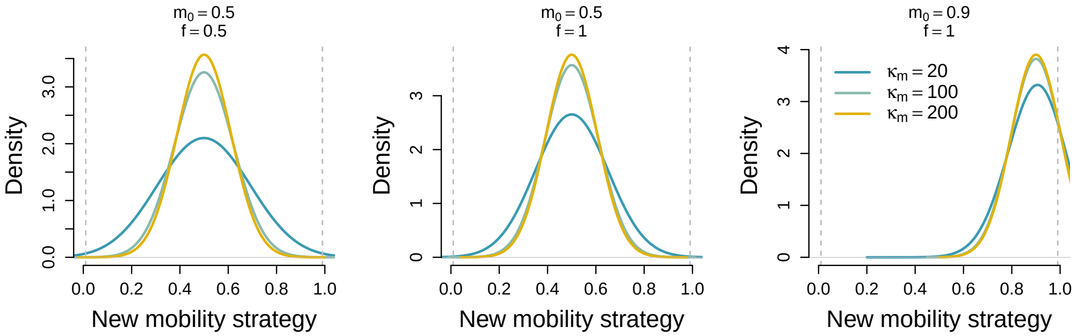


Figure 4.6: Examples of the distributions new mobility strategies would be selected from in strategy mutation. The agent's fitness, f, original mobility strategy, m_0, and the value of κ_m are varied. Dashed lines at 0.01 and 0.99 are shown.

randomly, and so to distinguish between the effects of selection and random drift, I introduce a 'null strategy'.

All agents have a null strategy, and is initialised, passed on, and mutated in exactly the same way as the mobility strategy. However, this is the extent of the null strategy – it has no effect in the model. Thus I can compare how the null strategy changes in comparison with the mobility strategy to see what is likely to be a real selection effect, and what is random drift in values.

4.5 Movement

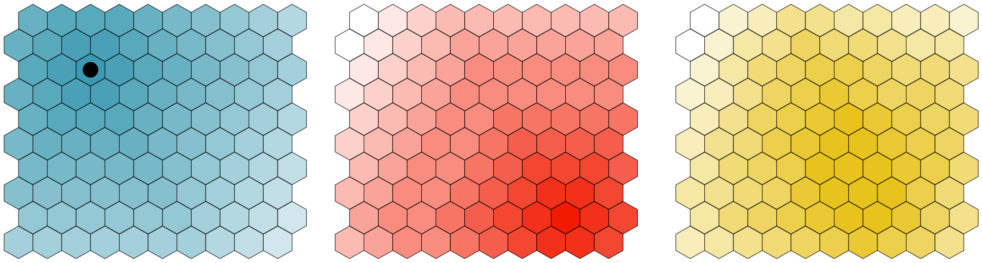
As mentioned previously, an agent will move site with a probability equal to its mobility strategy, m. If an agent does move site they are more likely to move to more 'attractive' sites. Site 'attractiveness' values are calculated based on proximity and the potential fitness for the agent, and are values between 0 and 1.

4.5.1 Distance Between Two Sites

The distance between two sites, here denoted as d, is the number of site steps between them. If (x_a, y_a, z_a) and (x_b, y_b, z_b) are the hexagonal coordinates of sites 'a' and 'b' respectively, then the distance between them is calculated as

$$d_{a,b} = \frac{|x_a - x_b| + |y_a - y_b| + |z_a - z_b|}{2}. \tag{4.12}$$

An example of distances from a site can be seen in Figure 4.7a.



(a) Distance **(b)** Potential fitness **(c)** Attractiveness

Figure 4.7: An example of the distances (a) from the original site (black circle), the potential fitnesses (b) and the attractiveness score calculated from these (c). Bolder colours represent the distance being closer (blue), or a higher fitness (red) or attractiveness (yellow).

4.5.2 Potential Fitness

The other factor that influences site attractiveness is the potential fitness, f^*, an agent could have there. For an agent considering moving to site b, this is

$$f_b^* = \frac{q_f^b}{n_b + 1}, \tag{4.13}$$

where q_f^b is the foraging quality of site b, and n_b is the number of agents at site b.

4.5.3 Attractiveness

Thus, taking proximity and potential fitness into account, the attractiveness of site b to an agent which was previously at site a is calculated as

$$A_b = (1 - \frac{d_{a,b}}{d_{max}}) \times f_b^*, \tag{4.14}$$

where d_{max} is the maximum distance possible in this region – calculated as the distance from the bottom left site to the top right. Thus when $d_{a,b} = d_{max}$ then $A_b = 0$, and thus attractiveness is relative to the region size. By inventing values for site potential fitnesses (Figure 4.7b), an example of the calculated site attractivenesses can be seen in Figure 4.7c.

The site the agent moves to is then picked weighted by these values (the algorithm used is shown in Appendix G).

4.5.4 Cost of Movement

Moving sites costs the agent an amount of fitness scaled by the distance it moves. If a family moves from site a to site b its new fitness is

$$f = f - \eta d_{a,b} \tag{4.15}$$

where η is the cost of movement parameter.

4.5.5 Site Size and the Maximum Number of Agents

I can estimate the size of the region I am modelling from the ethnographic data summarised in Table 2.5 of Chapter 2.

I found that the maximum total distance moved each year by the hunter-gatherer groups in the dataset given in Kelly (2013) is 1600 km. Therefore in my model I want the maximum possible distance moved in an iteration of the model to be less than or equal to 1600 km. The maximum number of moves possible in this model is given by the distance from opposite corners of the region, an illustration of this movement is given in Figure 4.8. The distance from the bottom left site (the first site) to the top right site (the final) site is

$$d_{1,f} = \frac{|x_1 - x_f| + |y_1 - y_f| + |z_1 - z_f|}{2}, \tag{4.16}$$

where (x_1, y_1, z_1) and (x_f, y_f, z_f) denote the coordinates for the first and final site respectively. Using basic trigonometry the distance from the centre of one hexagonal to the centre of a neighbouring hexagonal is $\sqrt{3}a$, where a is the length of a side of the hexagon.

Therefore in my model the following inequality should hold

$$(d_{1,f} - 1)\sqrt{3}a \leq 1600km. \tag{4.17}$$

The maximum population density of the hunter-gatherer data from Kelly (2013) is 2.665 persons/km^2 and the minimum is 0.004 persons/km^2. Thus I want my model to have a similar range in densities.

The maximum population density will occur when there are n_{max} agents at every site and the minimum will occur when there is one agent in the entire region. I will assume a family has four members, and therefore the number of people is 4 multiplied by the number of agents. Thus for the maximum population density

$$\frac{4n_{max}}{H} = 2.665 \text{ persons/km}^2 \tag{4.18}$$

and for the minimum population density

$$\frac{4}{s_x s_y H} = 0.004 \text{ persons/km}^2, \tag{4.19}$$

where H is the area of a hexagonal,

$$H = \frac{3\sqrt{3}}{2}a^2. \tag{4.20}$$

Having many agents and lots of sites in the model is computationally expensive, thus for most of my analysis I use a region of size 10×10. Thus, by rearranging Equation 4.19 this means that $H = 10$ km^2, and thus from Equation 4.18 I find $n_{max} = 6.66$ agents. Since we must have a discrete value for n_{max} and I want the population density to fall in the observed range of $[0.004, 2.665]$ persons/km^2 I will use $n_{max} = 6$ as a default value.

Using these values I can rearrange Equation 4.20 to find $a = 1.96km$. In a 10×10 region $d_{1,f} = 15$, and therefore the inequality 4.17 is satisfied ($(d_{1,f} - 1)\sqrt{3}a = 48$).

Thus using a 10×10 region I am modelling a region of 1000 km^2 which can theoretically support a maximum of 600 agents (although practically this will be limited by other parameters).

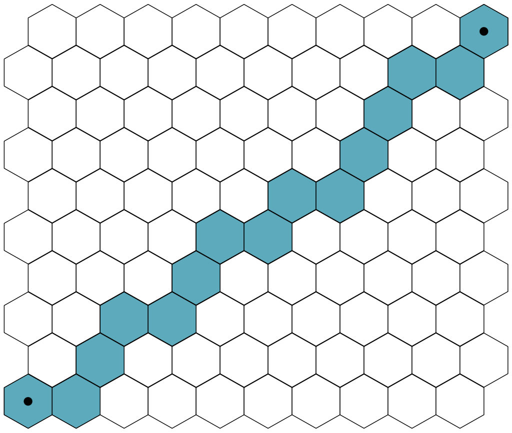


Figure 4.8: The furthest distance an agent can go in one iteration of the model.

4.6 Initialisation and Iterations

There are $\rho_{init} n_{max} s_x s_y$ agents in the initial iteration of the model, where ρ_{init} is the initial population density, and $n_{max} s_x s_y$ are the maximum number of agents possible in the region. These initial agents are all randomly assigned a site to occupy, their fitness is randomly assigned in $[\,f_{min}, 1]$, and their mobility strategy is randomly assigned in $[\,0.01, 0.99]$. The foraging qualities of sites are also randomly assigned in $[\,q_{f,min}, 1]$.

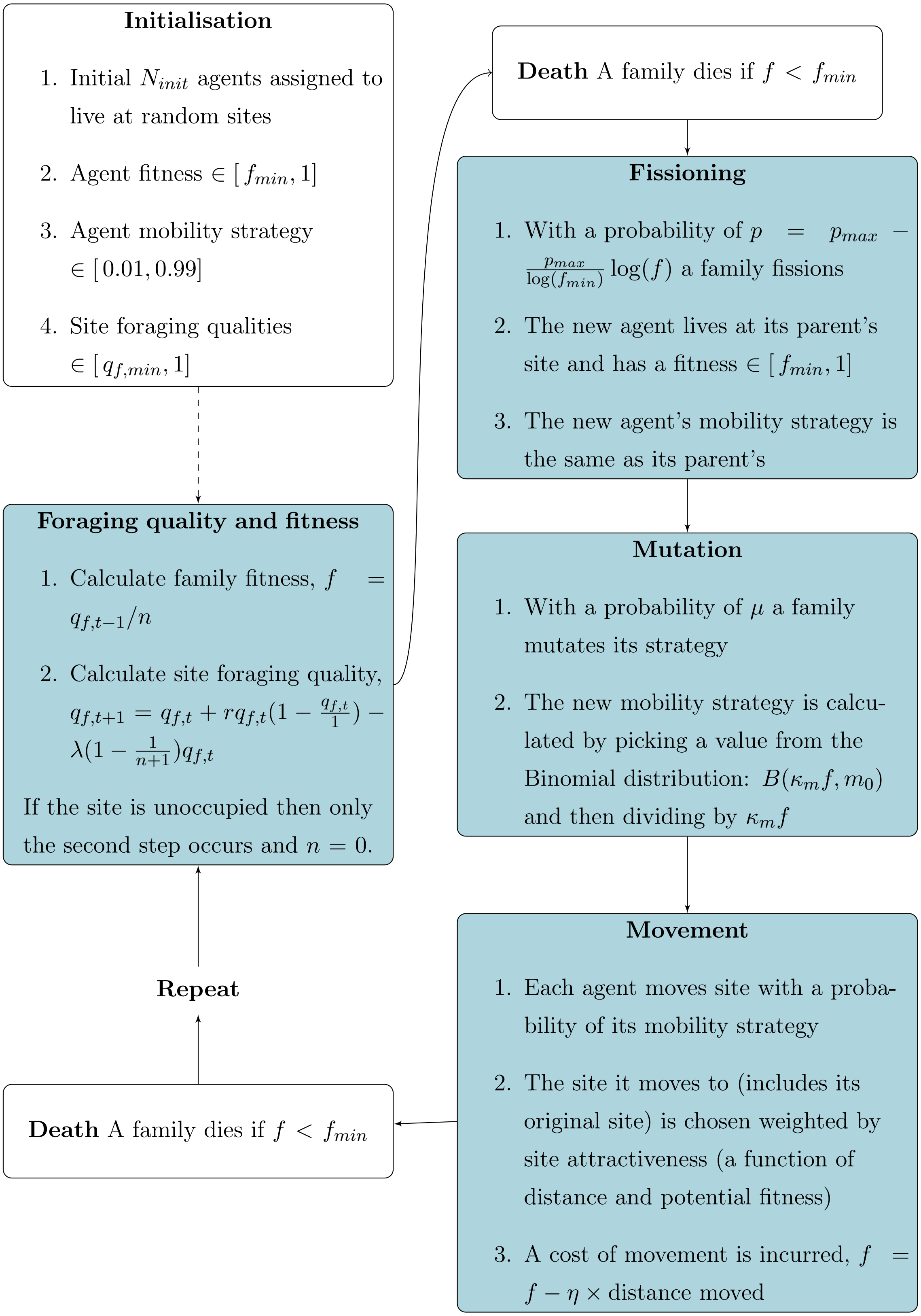
The 4 main steps to every iteration of the model are:

1. Foraging quality and fitness updates
2. Fissioning
3. Mutation
4. Movement

However after steps 1 and 4 there can also be the death of unfit agents.

At the beginning of each iteration the number of families, and all the information about the agents (their location, strategy and fitness) and the sites (who occupies it, the foraging quality) are saved. And after all the iterations have run I save the mean mobility strategy and fitness of all the agents left alive, or if the agents all die before the last iteration I save the iteration number at which the last agents died.

All the constants, variables and parameters in the Forager Model are given in Table 4.1, and the steps of the model are summarised in the flow diagram on page 144. In the next chapter I will discuss the results of running the Forager Model, and in Chapter 6 I will add the ability for agents to farm and discuss the results (the Forager-Farmer Model).



Initialisation

1. Initial N_{init} agents assigned to live at random sites
2. Agent fitness $\in [\,f_{min}, 1]$
3. Agent mobility strategy $\in [\,0.01, 0.99]$
4. Site foraging qualities $\in [\,q_{f,min}, 1]$

Foraging quality and fitness

1. Calculate family fitness, $f = q_{f,t-1}/n$
2. Calculate site foraging quality, $q_{f,t+1} = q_{f,t} + rq_{f,t}(1 - \frac{q_{f,t}}{1}) - \lambda(1 - \frac{1}{n+1})q_{f,t}$

If the site is unoccupied then only the second step occurs and $n = 0$.

Death A family dies if $f < f_{min}$

Fissioning

1. With a probability of $p = p_{max} - \frac{p_{max}}{\log(f_{min})}\log(f)$ a family fissions
2. The new agent lives at its parent's site and has a fitness $\in [\,f_{min}, 1]$
3. The new agent's mobility strategy is the same as its parent's

Mutation

1. With a probability of μ a family mutates its strategy
2. The new mobility strategy is calculated by picking a value from the Binomial distribution: $B(\kappa_m f, m_0)$ and then dividing by $\kappa_m f$

Movement

1. Each agent moves site with a probability of its mobility strategy
2. The site it moves to (includes its original site) is chosen weighted by site attractiveness (a function of distance and potential fitness)
3. A cost of movement is incurred, $f = f - \eta \times$ distance moved

Death A family dies if $f < f_{min}$

Repeat

Table 4.1: Constants, variables and parameters in the model.

Constants		Range
s_x	Number of sites in x axis	-
s_y	Number of sites in y axis	-
d_{max}	Maximum distance of the region	Distance between bottom left and top right site
$q_{f,min}$	Minimum foraging quality	-
N_{max}	Maximum number of families possible in the region	$n_{max}s_xs_y$
N_{init}	Total number of agents initially	$\rho_{init}n_{max}s_xs_y$
f_{min}	Death fitness	$1/n_{max}$
Variables		Range
q_f	Site foraging quality	$[\,q_{f,min}, 1]$
m	Agent mobility strategy	$[\,0.01, 0.99]$
f	Agent fitness	$[\,f_{min}, 1]$
p	Probability of fission	$[\,0, p_{max}]$
$d_{a,b}$	Distance between site a and b	$[\,0, d_{max}]$
f^*	Potential fitness at a site	$(0, 1]$
A	Attractiveness of a site	$[\,0, 1]$
n	Number of agents at a site	-
Parameters		Range
r	Foraging quality growth rate	$[\,0, 1]$
λ	Foraging quality depletion scalar	$[\,0, 1]$
κ_m	Mobility strategy conservatism	-
p_{max}	Maximum probability of fission	$[\,0, 1]$
η	Fitness cost of movement per site	$[\,0, 1]$
n_{max}	Maximum number of agents which can be supported at a site	≥ 1
μ	Probability of mutation	$[\,0, 1]$
ρ_{init}	Initial population density	$(0, 1]$

5

Mobility Changes in a Forager Population

Summary

Ethnographic data shows that there are many factors correlated with changes in hunter-gatherer mobility – including resource abundance and reliability, population density, dependence on fish, effective temperature, and dependence on farmed resources (see Sections 1.4 and 2.5.1). Since there are considerable energy costs to mobility (Hamilton et al., 2016) it is reasonable to assume there is some cost-to-benefit assessment of movement decisions. Therefore I can ask *what are the circumstances for high and low mobility?*

In this chapter I will explore the link between foraging and degrees of mobility using the Forager Model described in Chapter 4, with a particular focus on the transition from high to low mobility. To do this I perform various experiments using the model; each of which requires running the model with different parameters, variables and/or constants. A list of all my experiments is given in Table 5.1; this table can be cross-referenced to tables in the Appendix where all the model details are given. Methods and results are given in tandem in this chapter. Appendix C gives details of coding and running this model.

To illustrate the model dynamics and outcomes analysed in this chapter, I begin by giving an example of how I summarise outcomes from the model. In Section 5.2 I give the details of some preliminary checks I performed to confirm decisions made in the main analysis.

Section 5.3 gives details of running the Forager Model and the parameter sensitivity

analysis performed. In this analysis I find that large carrying capacities, large initial population densities, and low movement costs promote the evolution of low mobility in the model. I also find experimentation in mobility strategies and the potential for high amounts of fissioning make little difference to outcomes, suggesting that stable strategies have evolved in the duration of my simulation experiments. Furthermore, the ratio between the two parameters which directly effect foraging quality – the growth rate and depletion rate, have a strong impact on model outcomes, where in general the best environmental conditions (highest growth rate and lowest depletion rate) give rise to decreased mobility. I also show that simulations roughly fall into a continuum between having low numbers of agents, high fitnesses and high mobility strategies, and having high numbers of agents, low fitnesses and low mobility strategies.

I look at the effect of spatial and temporal environmental variability in Section 5.4; for this I find that temporal variability discourages low mobility in my model, but spatial variability allows both high and low mobility strategies to co-occur in the simulation. In Section 5.5 I look at the how simulations change over time – I find that when a population changes from having initially high mobility strategies to having low mobility strategies in the final iteration, mean mobility will usually start to decrease before the number of agents start to increase. I discuss the results of this chapter in Section 5.6.

Table 5.1: A brief description of experiments using the foraging only model. The table numbers refer to tables in Appendix H.

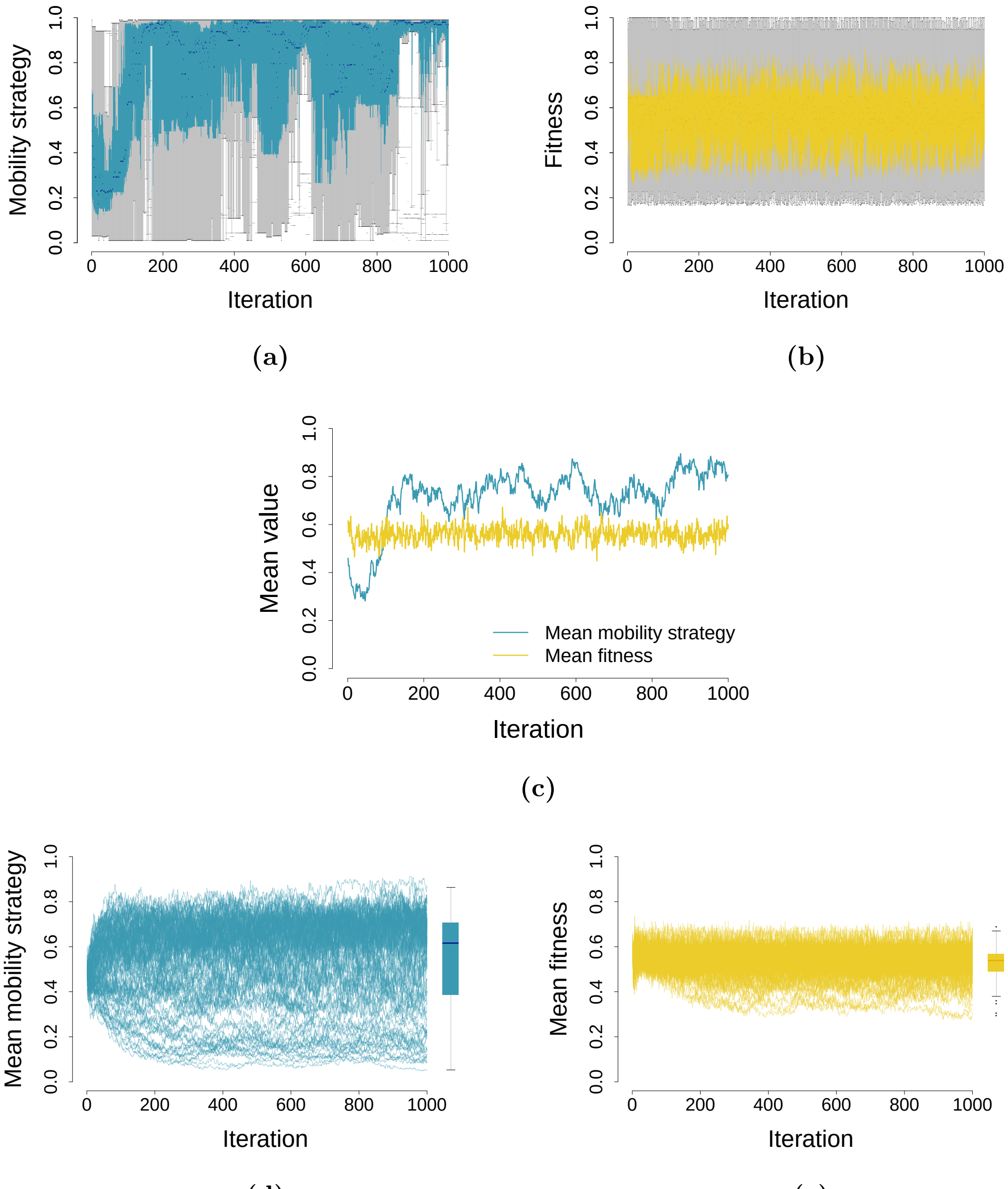
Experiment number	Description	Table
1	The effects of initial conditions	H1
2	The effects of number of iterations	H2
3	The effects of the number of sites	H3
4	Using the average as a summary	H4
5	Varying all 8 parameters	H5
6	Varying 4 parameters	H6
7	Varying 2 parameters	H7
8	Looking at temporal variability	H8
9	Looking at spatial variability	H9
10	Simulations over time	H10

5.1 An Example of Model Outcomes

When I run a simulation of the Forager Model I input how many iterations it should run for and how many simulations I want to run (as well as the values for parameters and constants). I refer to a 'simulation' as an independent run of the model. There is unique data for every iteration of each simulation – the location, fitness, and strategies of every agent, and the foraging quality of every site. I refer to this data as the model outcomes. Figures 5.1a and 5.1b show the distributions of mobility strategies and fitnesses in the agents at each iteration for one simulation of the model. I can summarise the model outcomes by finding the mean values for agents and sites, i.e. the mean fitness of all agents at each iteration in a single simulation of the model. Figure 5.1c shows an example of this. With this data I can see how population averages change over time.

Since there is stochasticity in the model, every simulation will have different dynamics even if the conditions are the same. Therefore, I run many simulations of the model to understand the model behaviour in general. Figures 5.1d and 5.1e show the mean mobility strategies and fitnesses over time for 100 simulations of the model, with the final mean values for all the simulations also shown in a box plot. I am mostly (but not always) interested in seeing the final iteration conditions (e.g. what conditions lead to low mobility after some time) rather than the dynamics over time. Hence, for much of the analysis presented here I compare the final mean mobility strategy (or other final outcomes) for different conditions.

Note that outcomes of the model are saved at the end of every iteration, and so the data recorded for iteration '0' is not the same as the initial conditions of the model.



(a)

(b)

(c)

(d)

(e)

Figure 5.1: Box plots of the mobility strategies (a) and fitnesses (b) of all agents at each iteration using one simulation, the means of these are given in (c). The mean mobility strategies and fitnesses for 100 simulations are plotted in (d) and (e), with the final mean outcomes also given in a box plot. For box plots the interquartile range is shown in blue or yellow (for mobility strategy and fitness respectively), the median is shown in slightly darker blue or yellow, the whiskers are in grey and outliers in black.

5.2 Preliminary Checks

My main interest is to investigate the effect of the parameters (given in Table 4.1) on the outcomes of the model after a number of iterations. However, the model outcomes may also be dependent on the values I have chosen for the constants of the model. Therefore in this section I will investigate the effect of (and attempt to justify default values for) the initial conditions of the model, the number of iterations the model is run for, the region size, and the minimum foraging quality. The constants and parameters used and varied for these experiments are given in Tables H1, H2 and H3 of Appendix H.

For the region size and the number of iterations in the model, there is a trade off between making sure that the values selected for these are large enough to give accurate and reproducible results, but not so large that the memory and time these simulations will need is impractical.

5.2.1 Initial Conditions – Experiment 1

I ran the model 1000 times each with 100 random sets of initial conditions (thus the model was run $100,000$ times in total) for 1000 iterations. Initial conditions in the model are the fitness, mobility and null strategies of the agents, the sites the agents live at, and the site qualities at iteration 0. For these runs I randomly varied $r \in [0,1]$ and $\lambda \in [0,1]$. I set $\kappa_m = 100$, $p_{max} = 0.14$, $\eta = 0.05$, $n_{max} = 6$, $\mu = 0.04$, and $\rho_{init} = 0.1$.

In Figure 5.2 I show the ranges of five different model outcomes for each of the 100 sets of simulations. Table 5.2 gives the correlation coefficients between initial and final conditions. From these it can be seen that the difference the initial conditions make to the end results are generally quite small (with the exception of the initial and final mean null strategy) – the interquartile ranges are mostly overlapping, and the correlation coefficients are small. Hence I will not consider the initial conditions in further analysis of the model and generate them randomly for each run of the model.

5.2.2 Number of Iterations – Experiment 2

The number of iterations (where one iteration models one year) to run the model for is also something to consider. If there is a stable state for the system then I need to run the model for enough iterations for this stable state to be reached. To investigate the number of iterations needed I ran the model 1000 times over 2000 iterations and recorded the mean agent and site properties every 100 iterations. For these I randomly varied $r \in [0,1]$, $\lambda \in [0,1]$, and set $\kappa_m = 100$, $p_{max} = 0.14$, $\eta = 0.05$, $n_{max} = 6$,

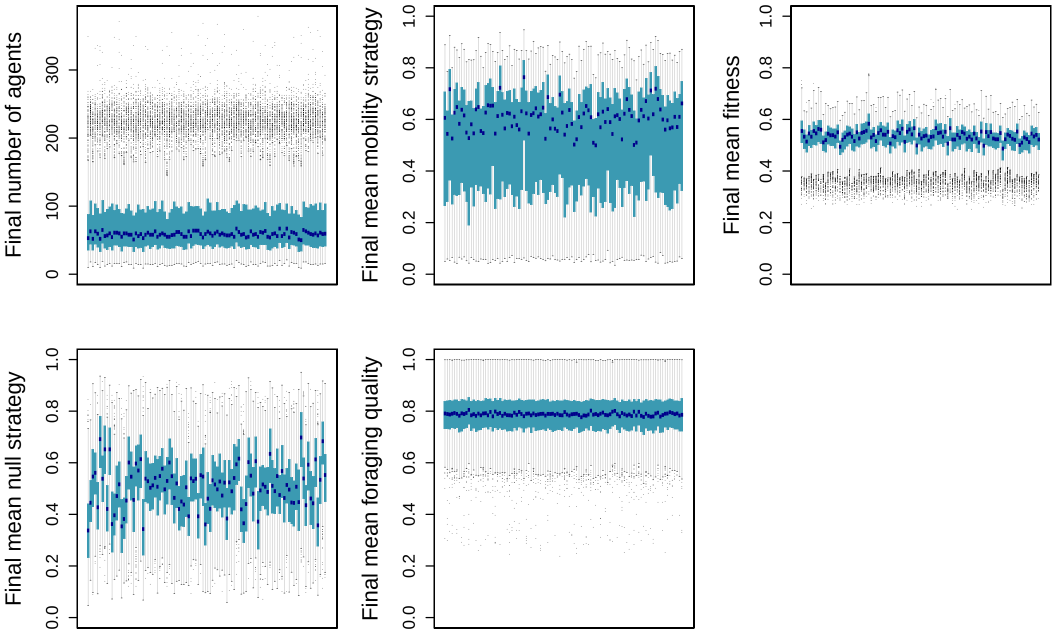


Figure 5.2: A comparison of the spread of model outcomes of 1000 simulations with the same initial conditions, for each of the 100 initial condition sets (each box plot). Medians are given in dark blue, and the inter-quartile range in a lighter blue.

Table 5.2: Pearson product-moment correlation coefficients between initial and final iteration conditions. Using all 100,000 simulations. ns – the tests which were not significant (p-value ≥ 0.05).

	Initial mean fitness	Initial mean mobility strategy	Initial mean null strategy	Initial mean foraging quality
Final number of agents	0.005^{ns}	-0.009	-0.001^{ns}	-0.001^{ns}
Final mean mobility strategy	-0.011	0.049	0.016	-0.005^{ns}
Final mean fitness	0.108	0.01	0.011	0.046
Final mean null strategy	0.007	-0.07	0.213	0.039
Final mean foraging quality	-0.01	0^{ns}	-0.004^{ns}	-0.005^{ns}

$\mu = 0.04$, and $\rho_{init} = 0.1$.

Figure 5.3 shows how the distribution of simulation outcomes converge over time. Although the range is always large, the median value converges as the number of iterations increases. Using the method described in Section 2.4.3 I compared the outcomes of simulations at consecutive pairs of iterations (e.g. comparing the distributions of mean mobility strategies at iteration 200 and 300) to see if these distributions become more similar. As I compare later iterations the p-values become larger, and therefore the distribution means are likely to be converging; these values are shown in Figure 5.4.

From this analysis it appears that running the model for 1000 iterations would be enough time for stable behaviour of the system to appear.

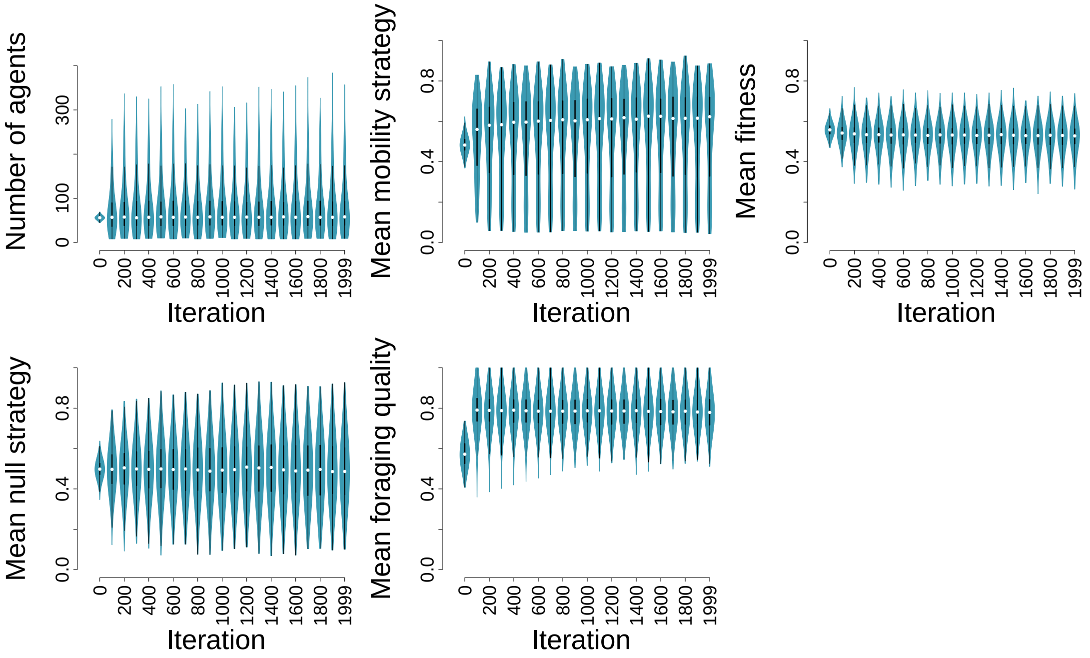


Figure 5.3: Violin plots of model outcomes at various iterations of 2000 simulations.

5.2.3 Number of Sites – Experiment 3

I was not sure what effect the number of sites would have on the model outcomes, so I compared the outcomes from six different region sizes. The region sizes compared were 8×8, 9×9, 10×10, 11×11, 12×12 and 20×20. I randomly varied $r \in [0, 1]$, $\lambda \in [0, 1]$ and set $\kappa_m = 100$, $p_{max} = 0.14$, $\eta = 0.05$, $n_{max} = 6$, $\mu = 0.04$, and $\rho_{init} = 0.1$. I varied the model 1000 times each for 1000 iterations for each of these region sizes.

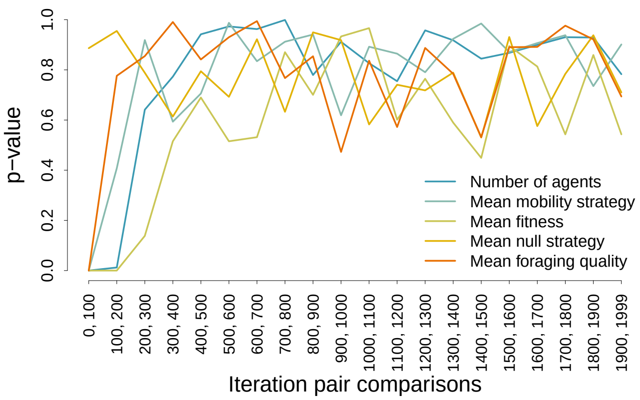


Figure 5.4: The p-values from a two-tailed Student's t-test on 5 simulation outcomes at two consecutive iterations. e.g. I perform a t-test on the mean mobility strategies in 1000 simulations at iteration 200 and 300 and plot the p-values.

Figure 5.5 shows the range of some of the final properties of the model for each of the different region sizes. I note that as the region size increases the final number of agents increases, which makes sense as there is more space for agents. I also find that the final mean foraging quality increases with region size – possibly because of less depletion since there is more space for agents. Generally however, the range of values become tighter (due to the law of large numbers), but median values do not change much. Hence I will use a region size of 10×10.

5.2.4 Minimum Foraging Quality

The reason I have a minimum foraging quality in the model is to make sure that it never reaches 0 (since if it reaches 0 it would never be able to recover due to the nature of the equation for foraging quality). Therefore the only real criterion for this value is that it should be > 0 and ≤ 1.

It makes sense that there will be a natural value for $q_{f,min}$ which occurs simply from the dynamic that there will be no depletion from foraging if the foraging quality has become so low that all the agents die. However specifying this natural minimum value is difficult since there are many options for how the simulations play out. As long as my inputted value for $q_{f,min}$ is lower than the natural minimum then I should not have to worry that the value for $q_{f,min}$ is biasing my results.

In all the simulations run in this section I chose $q_{f,min} = 0.1$ and I found that the minimum final mean foraging quality that ever occurred was 0.238. This does not mean

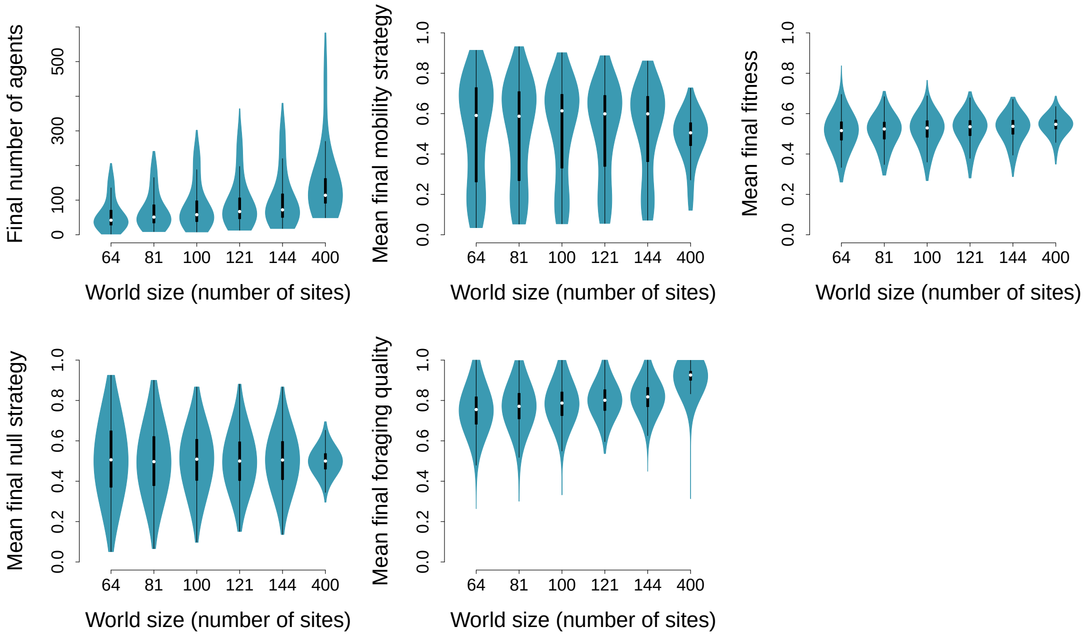


Figure 5.5: Violin plots of the final properties of simulations for different region sizes.

that there was not a point during the simulations when the foraging quality became less than 0.1 (and then had to be reset to 0.1), but 0.238 is encouragingly greater than 0.1 to suggest that the use of $q_{f,min} = 0.1$ is adequate.

5.2.5 Averaging – Experiment 4

In the analysis in this chapter I use the final mean mobility strategy as the measure of how mobile the population is. To double check whether it is reasonable to summarise the final population using the mean, I look at the final distributions of all mobility strategies in the final population. I ran the model 1000 times over 1000 iterations with random values for r and λ.

Figure 5.6 shows the relative frequencies of mobility strategies of the final agent population coloured by the mean mobility strategy of the population, for each of the 1000 simulations. The absence of a yellow peak around 0.5 in this plot indicates that when the mean mobility strategy is at a mid value, it is the case that the agents have a wide range of strategies, as opposed to every agent having a strategy of around 0.5.

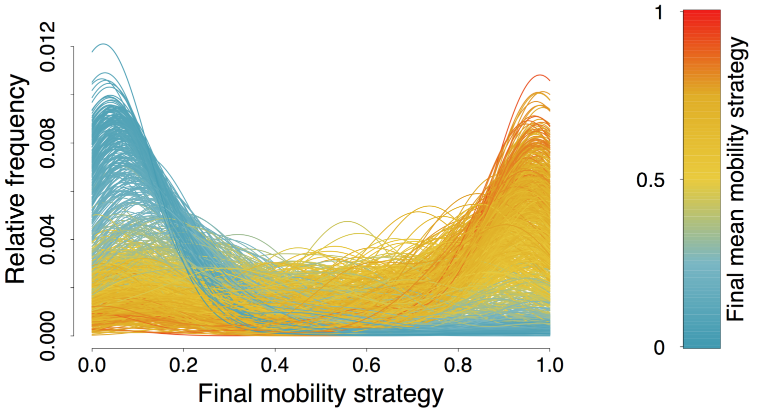


Figure 5.6: Relative frequencies of mobility strategies in the final agent populations of 1000 simulations, coloured by the mean value.

5.2.6 Outcomes of Preliminary Checks

The analysis performed in this section leaves me confident that I am not biasing my interpretation of the results by picking random initial conditions for every run of the model, by using a region size of 10×10, by setting $q_{f,min} = 0.1$, or by running the model for 1000 iterations. This means that I can focus on analysing the other parts of the model exclusively. The analysis also shows that caution must be applied when interpreting final mean mobility strategies of around 0.5, as rather than this meaning that most agents have mobility strategies of around 0.5, it is likely to mean their strategies are distributed widely in the range of 0 to 1.

5.3 Parameter Sensitivity and Simulation Outcomes

To thoroughly explore the parameter space of the model I ran it many times with randomly chosen parameter values and recorded certain outcomes of the simulations. The simulation outcomes I record are the final number of agents, the mean of the mobility and null strategy, fitness, and foraging quality in the final iteration. I only consider simulations in my analysis which have ≥ 15 agents alive in the final iteration (which happens more than 97% of the time anyway), since otherwise taking the mean of such a small sample can include too much noise. Thus, unless otherwise stated these are the subset of simulations analysed in this chapter.

With the data of parameter values and the five outcomes for many independent simulations, I can then investigate which parameter values influence certain model outcomes.

To look at how parameters affect certain outcomes in my model I can use two approaches: the FIO method (proposed in Section 2.4.1 and used in my analysis of the Bowles and Choi model in Chapter 3); or the OC method which searches for unspecified outcome types discussed in Section 2.4.4. If I use the FIO method I can use either low or high mobility as my idealised outcome, and then investigate the simulations which have the highest and lowest mobility, to see what the environmental conditions are most likely to be in either case. However, since there are simulation outcomes other than final mean mobility, which are possibly correlated and still worth investigating (e.g. the number of agents, mean fitness, etc.), using the OC method allows a less forced and more broad analysis of combined parameter value effects on simulation outcomes. With this method I look at all the outcomes of the simulations and see if there are any simulation outcome groupings. This allows me to look more thoroughly at model complexity without being biased by looking for a particular outcome.

In this section I will discuss the experiments and results when running many simulations and varying all eight, four and two of the parameters.

5.3.1 The Effects of All 8 Parameters – Experiment 5

I ran the model 100,000 times whilst varying the values of all 8 parameters; the details of this experiment are given in Table H5. Of these, 3112 simulations had no agents in the final iteration (they had all died) and 62,089 simulations had ≥ 15 agents alive in the final iteration. Figure 5.7 shows that the simulations in which all agents died before the final iteration were those with the lowest initial population density, the lowest maximum number of agents which can be supported at a site, and high movement costs.

Figure 5.8 shows the outcomes of the simulations with ≥ 15 agents alive in the final iteration. I note that the distribution of final mobility strategies is not Gaussian, and therefore there does appear to be some differences in the simulations (whether from the parameter combinations or to do with the stochasticity of the simulation) which lead to different outcomes. I examine the relationship between parameter values and final mean mobility strategy with scatter plots (Figure 5.9, correlation coefficients are given in Table 5.3). From these plots I note that the final mean mobility strategies are often correlated with parameter values. For example, the cost of movement (η) is never high in the simulations with a high mean mobility, and the depletion rate is never high in the simulations with a low mean mobility.

I performed a principal components analysis on four outcomes (I ignored the final null strategy). Principal component 1 (PC1) accounts for 41.3% of variation, PC2 accounts for 35.5%, PC3 accounts for 15.8%, and PC4 accounts for the remaining 7.4%. Each pair of principal components is visualised in Figure 5.10.

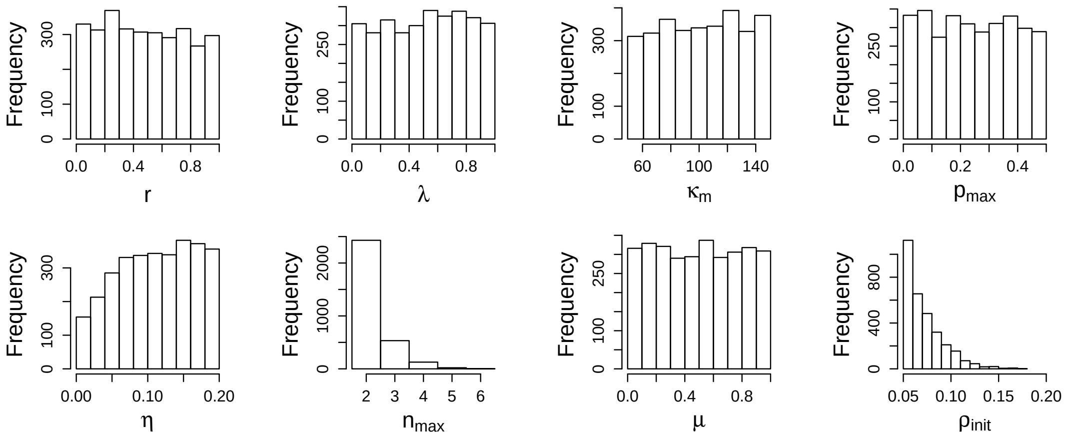


Figure 5.7: Histograms of parameter values in the 3112 simulations with no agents alive in the final iteration. When all parameters are varied.

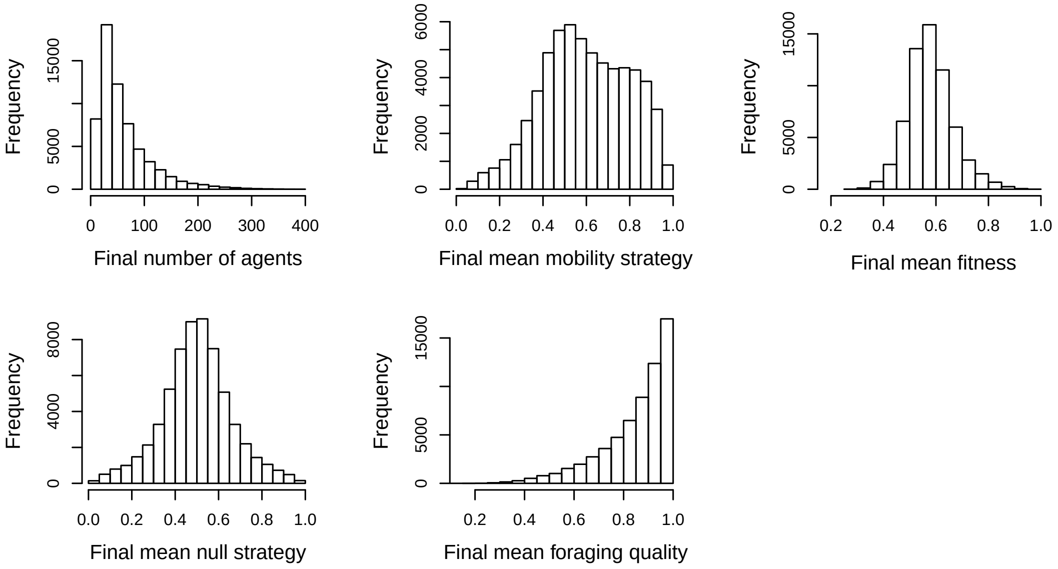


Figure 5.8: Histograms of simulation outcomes in the 62,089 simulations with ≥ 15 agents alive in the final iteration. When all parameters are varied.

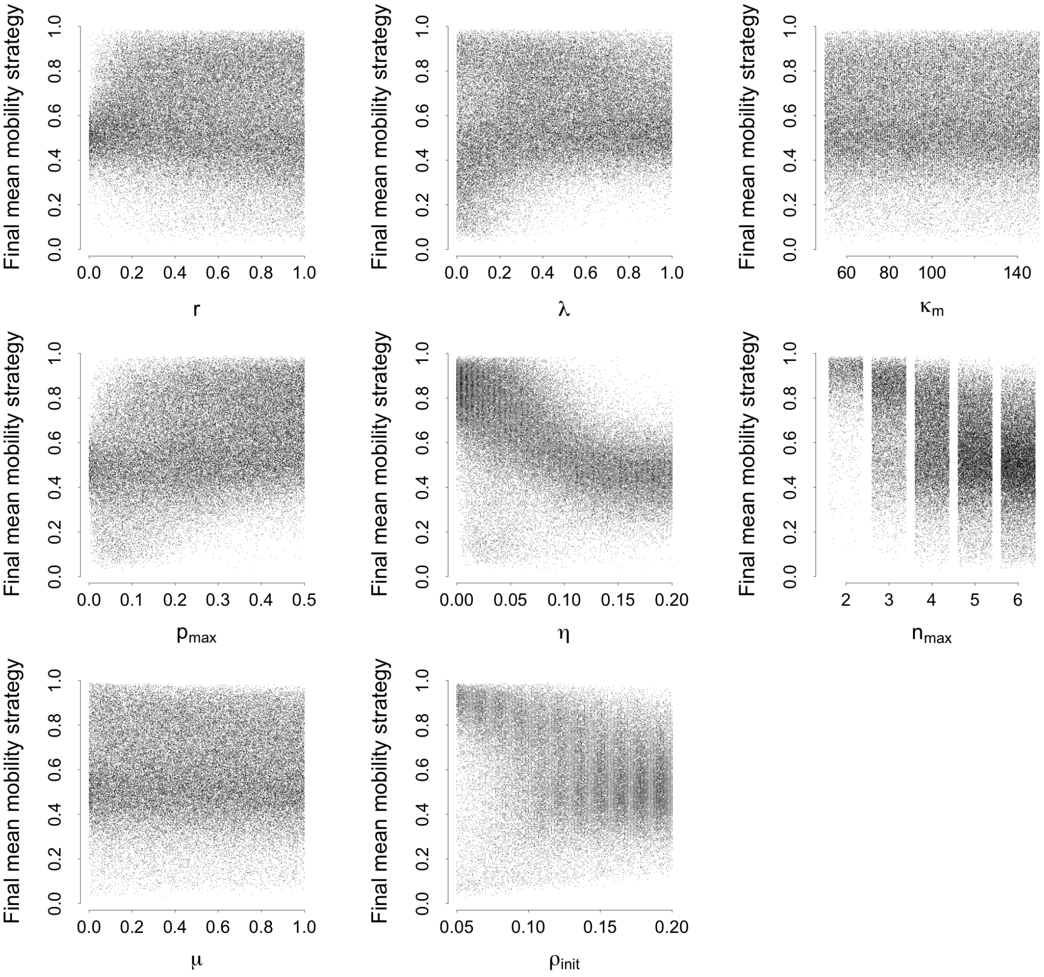


Figure 5.9: Scatter plots of the parameters values and final mean mobility strategies in the 62,089 simulations with ≥ 15 agents alive in the final iteration. When all parameters are varied.

Table 5.3: Pearson product-moment correlation coefficients for every combination of parameters and outcomes in the 62,089 simulations with $\geq$ 15 agents alive in the final iteration. When all parameters are varied. All correlations > $|0.07|$ are significant (p-value < 0.05).

	r	λ	κ_m	p_{max}	η	n_{max}	μ	ρ_{init}	Initial mean mobility strategy	Initial mean null strategy	Final number of agents	Final mean mobility strategy	Final mean fitness	Final mean null strategy
r														
λ	0.03													
κ_m	0	-0.001												
p_{max}	0.007	0	0											
η	-0.016	-0.006	0	0.022										
n_{max}	-0.057	0.094	0	-0.08	0.226									
μ	0	-0.002	0.003	-0.002	-0.004	-0.007								
ρ_{init}	-0.069	0.076	-0.002	-0.06	0.184	-0.094	0.004							
Initial mean mobility strategy	0.001	0.002	0.004	0.004	-0.005	-0.01	-0.003	-0.002						
Initial mean null strategy	-0.001	0.003	0	-0.001	-0.001	0.002	-0.006	0.001	-0.002					
Final number of agents	0.232	-0.353	0.001	0.182	-0.391	0.311	0.002	0.057	-0.007	0.001				
Final mean mobility strategy	-0.004	0.136	0.007	0.279	-0.527	-0.413	-0.012	-0.269	0.038	0.006	-0.054			
Final mean fitness	-0.025	0.055	0.003	-0.093	-0.076	-0.737	0.002	0.125	0.008	0	-0.498	0.325		
Final mean null strategy	0.005	-0.003	0.001	0.002	0.001	0	0.001	-0.007	0.012	0.05	0.005	0.001	-0.002	
Final mean foraging quality	0.294	-0.354	0.004	-0.207	0.573	-0.189	0.001	0.045	-0.004	-0.002	-0.166	-0.402	0.246	0.004

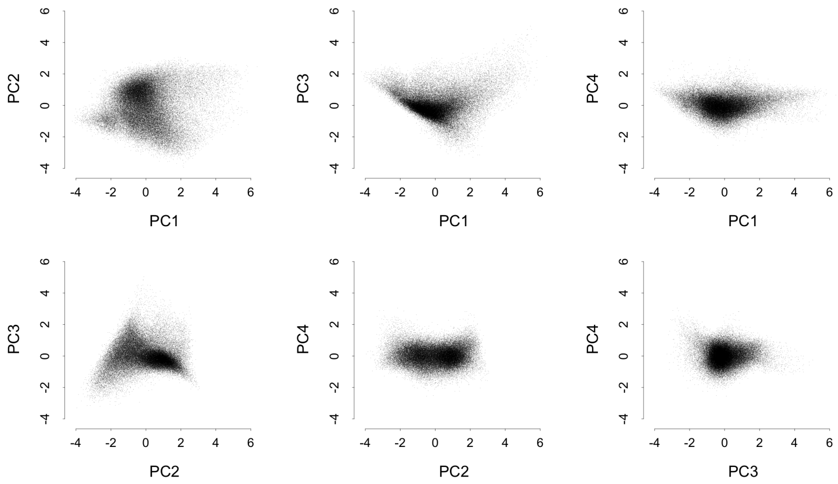


Figure 5.10: Each pair of principal components from the four main outcomes of 62,089 simulations with ≥ 15 agents alive in the final iteration.

Outcome Clusters

Since some of the simulation outcomes were highly correlated (final number of agents, final mean mobility, fitness and foraging quality) I looked for clusters in these outcomes, rather than just separating the simulations by whether they have a high or low mobility. This Outcome Clustering (OC) method is described in Section 2.4.4.

First, I looked at whether clusters in the outcomes were noticeable by eye. I plotted scatters of each pair of outcomes and coloured each point by a third outcome; this is shown in Figure 5.11. These plots show that although there are no obvious clusters, there is some structure to the types of simulation (seen by some gradient to the colours).

Due to processing taking a long time, I found outcome clusters based only on the first 10,000 simulations and then used these to predict the rest of the cluster classifications using the function ‘predict.Mclust’, also in the ‘mclust’ library.

I have plotted the relative densities of outcomes for each of these clusters (9 were found) in Figure 5.12a, and in Figure 5.12b I have plotted pairs of outcomes coloured by cluster. From these figures it can be seen that the clusters are roughly a continuation of two extreme types, which I will henceforth refer to as States ‘A’ and ‘B’: one extreme state has low numbers of agents, high mobility strategies, high fitnesses and low foraging qualities (the red cluster, State A); and the other has the opposite, high numbers of agents, low mobility strategies, low fitnesses and high foraging qualities (the blue cluster, State B).

I also plotted relative densities of the parameter values in each of the clusters in Figure 5.13. I found that certain parameter values make little or no difference to which cluster the simulation is assigned to – which can be seen by the same relative density pattern in all clusters. This is the case for the parameters concerning the mutation of strategies; κ_m and μ. I discuss how mutation has little effect on outcomes in my model by setting $\mu = 0$ in Appendix I. I can also see when parameter values do make a difference to which cluster a simulation is assigned to – which is seen by different relative density patterns for clusters. For example, this is the case for the maximum number of agents, n_{max}, where State A outcomes have lower values (but not too low) and State B outcomes have high values.

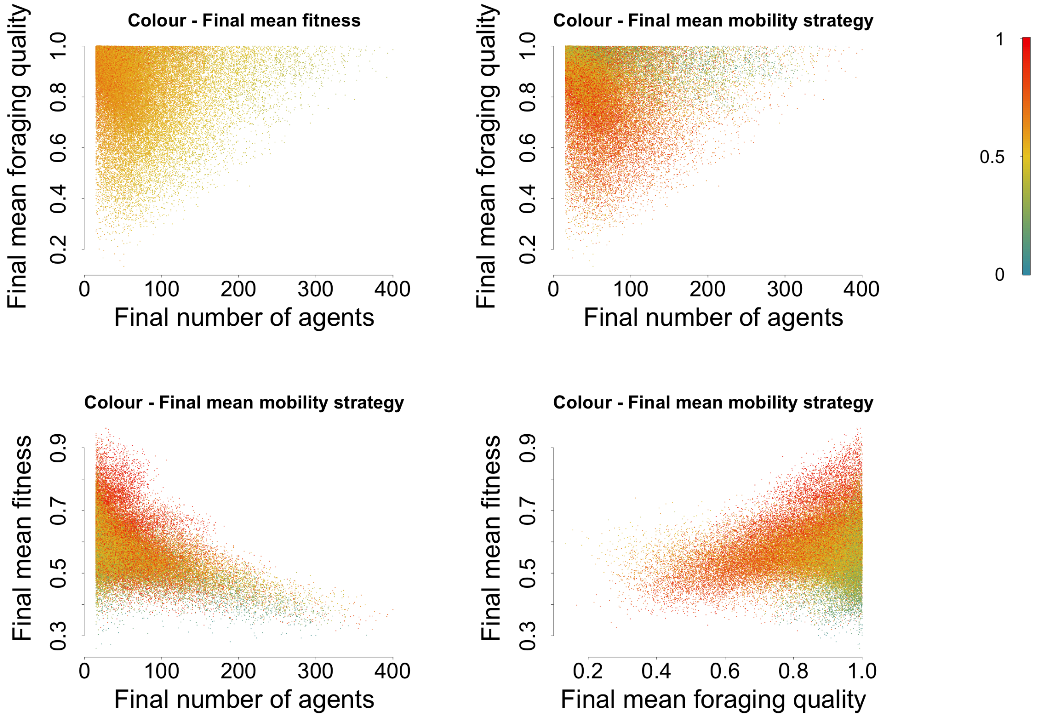
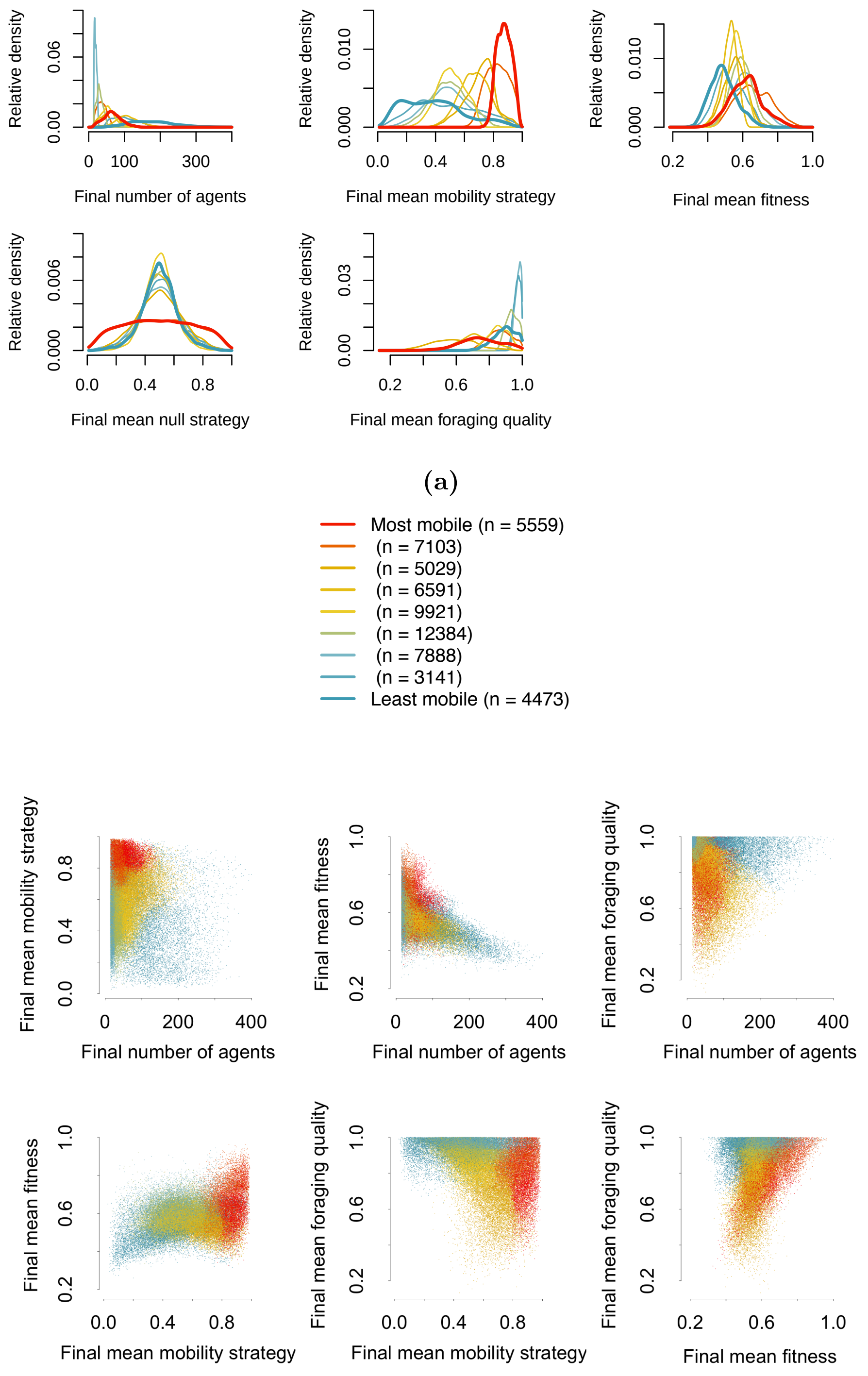


Figure 5.11: 3D representations of 3 outcomes (x and y axis, and colour) in the 62,089 simulations with $\geq$ 15 agents alive in the final iteration.



(a)

(b)

Figure 5.12: The outcomes in the different clusters, using all the 62,089 simulations with ≥ 15 agents alive in the final iteration when all parameters are varied. (a) Outcomes in different clusters. The most and least mobile clusters are highlighted with a thicker line. (b) Outcome pairs coloured by cluster.

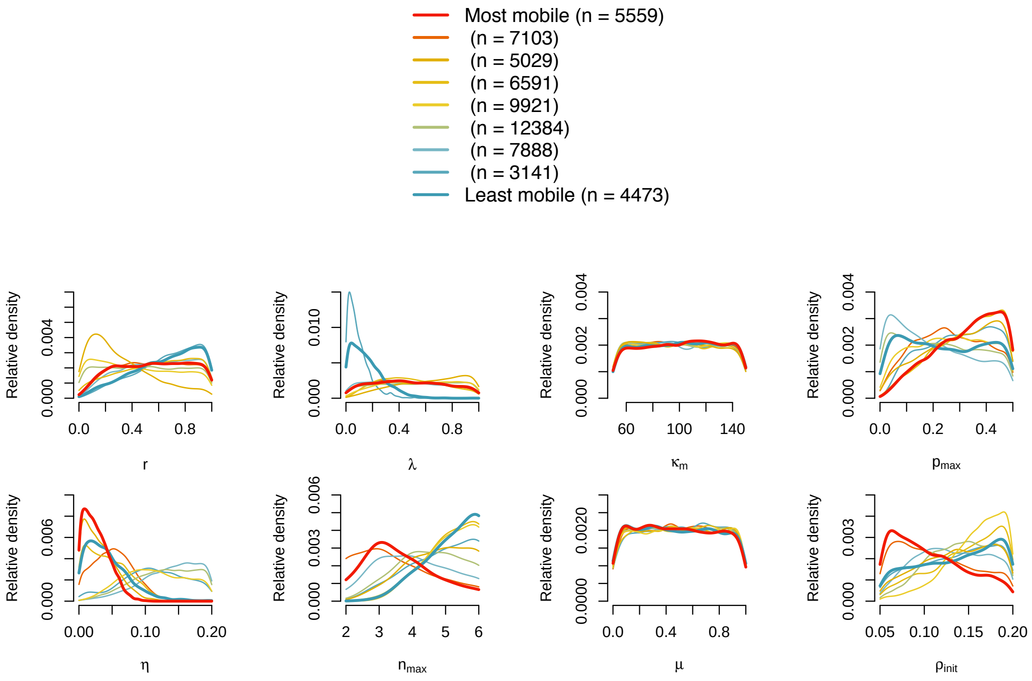


Figure 5.13: The parameters in the different clusters, using all the 62,089 simulations with ≥ 15 agents alive in the final iteration when all parameters are varied. The most and least mobile clusters are highlighted with a thicker line.

5.3.2 Fixing Certain Parameters – Experiments 6 and 7

Varying all the parameters can make the analysis less clear – since there are more interdependencies and effects to consider – and introduces more noise into the model. Since some of the parameters are of greater interest than others, and some have values backed up from observed data (namely p_{max}, n_{max} and μ – discussed in Chapter 4), I chose to run the simulations again but this time fixing some of the parameter values.

I varied the four parameters r, λ, p_{max} and η in one experiment since these both had a strong impact on simulation outcomes and I wanted to investigate their effect further. I also ran an experiment whilst only varying the parameters to do with foraging quality growth and depletion (r and λ) to more clearly understand the effect of the environment. When I only varied r and λ I set p_{max} to its default value of 0.14 (as explained in Section 4.3.1), and the cost of movement η to 0.05.

I chose to no longer vary n_{max} and ρ_{init}, since I suspect they mostly directly affect the numbers of agents (which may then indirectly effect the other outcomes), and I would rather investigate parameters with indirect effects on the evolution of certain outcomes. I set n_{max} to its default value (of 6, shown in Section 4.5.5) and ρ_{init} to 0.1.

In Section 5.3.1 I showed that the value for κ_m makes little difference to simulation outcomes, therefore varying it is unnecessary, and thus I fix it to a mid value of $\kappa_m = 100$. This is also the case for μ, and thus I chose the default value of $\mu = 0.04$ as explained in Section 4.4.

Simulation Outcomes

Of the 100,000 simulations run 95,835 had ≥ 15 agents alive in the final iteration when varying four parameters and 98,657 when varying two parameters. I compared the outcomes of these simulations, along with those when 8 parameters were varied, in Figure 5.14. I note from this that varying fewer parameters gives more of the simulations with lower mobilities, although there is not a large difference between varying 8 and 4. There is however a stark difference in the final mean mobility strategies density when only 2 parameters are varied – for this a clear bimodal distribution can be seen.

Pearson's product-moment correlation coefficients between parameters and outcomes when four and two parameters are varied are given in Table 5.4 and 5.5 respectively. Correlations are of the same sign, but become stronger when fewer parameters are varied. As in Figure 5.11 I can look at each triplet of the highly correlated outcomes to see if there are any obvious clusters, these are shown in Figures 5.15a and 5.15b – for these the clusters are clearer than when all eight parameters are varied.

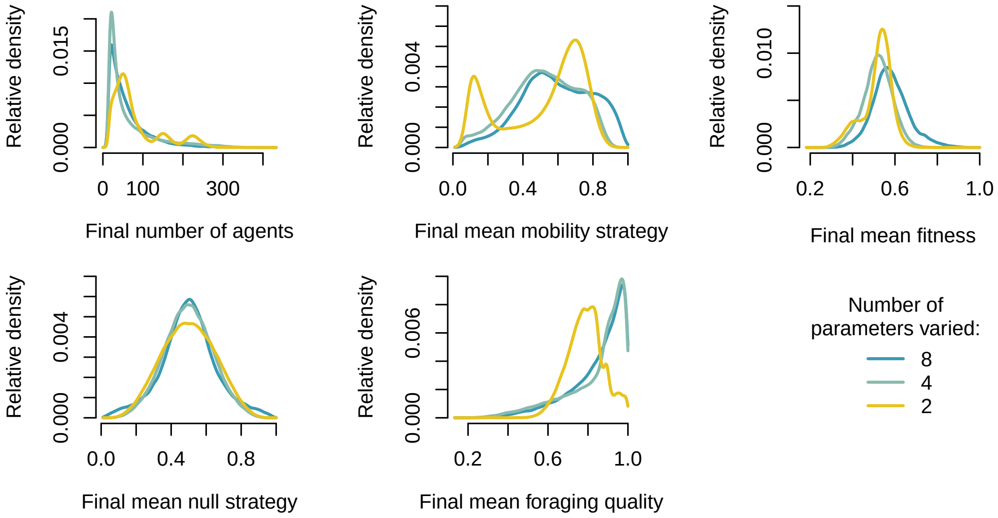


Figure 5.14: Relative densities of the outcomes of simulations with ≥ 15 agents alive in the final iteration, when eight (62,089 simulations), four (95,835 simulations) and two (98,657 simulations) of the parameters are varied.

Table 5.4: Pearson product-moment correlation coefficients for every combination of parameters and outcomes in the 95,835 simulations with ≥ 15 agents alive in the final iteration. When four parameters are varied. All correlations $> |0.06|$ are significant (p-value < 0.05).

	r	λ	p_{max}	η	Initial mean mobility strategy	Initial mean null strategy	Final number of agents	Final mean mobility strategy	Final mean fitness	Final mean null strategy
λ	0.012									
p_{max}	-0.006	0.01								
η	0.015	-0.009	0.021							
Initial mean mobility strategy	-0.002	0.003	0.002	-0.001						
Initial mean null strategy	0.003	-0.004	-0.004	-0.006	0.002					
Final number of agents	0.287	-0.465	0.182	-0.555	-0.005	0.005				
Final mean mobility strategy	-0.138	0.401	0.281	-0.31	0.122	0.001	-0.178			
Final mean fitness	-0.23	0.358	-0.155	0.357	0.027	-0.006	-0.663	0.155		
Final mean null strategy	0.004	-0.001	0	0.004	-0.003	0.226	-0.002	-0.002	0.001	
Final mean foraging quality	0.239	-0.259	-0.218	0.714	-0.003	-0.003	-0.148	-0.602	0.207	0.006

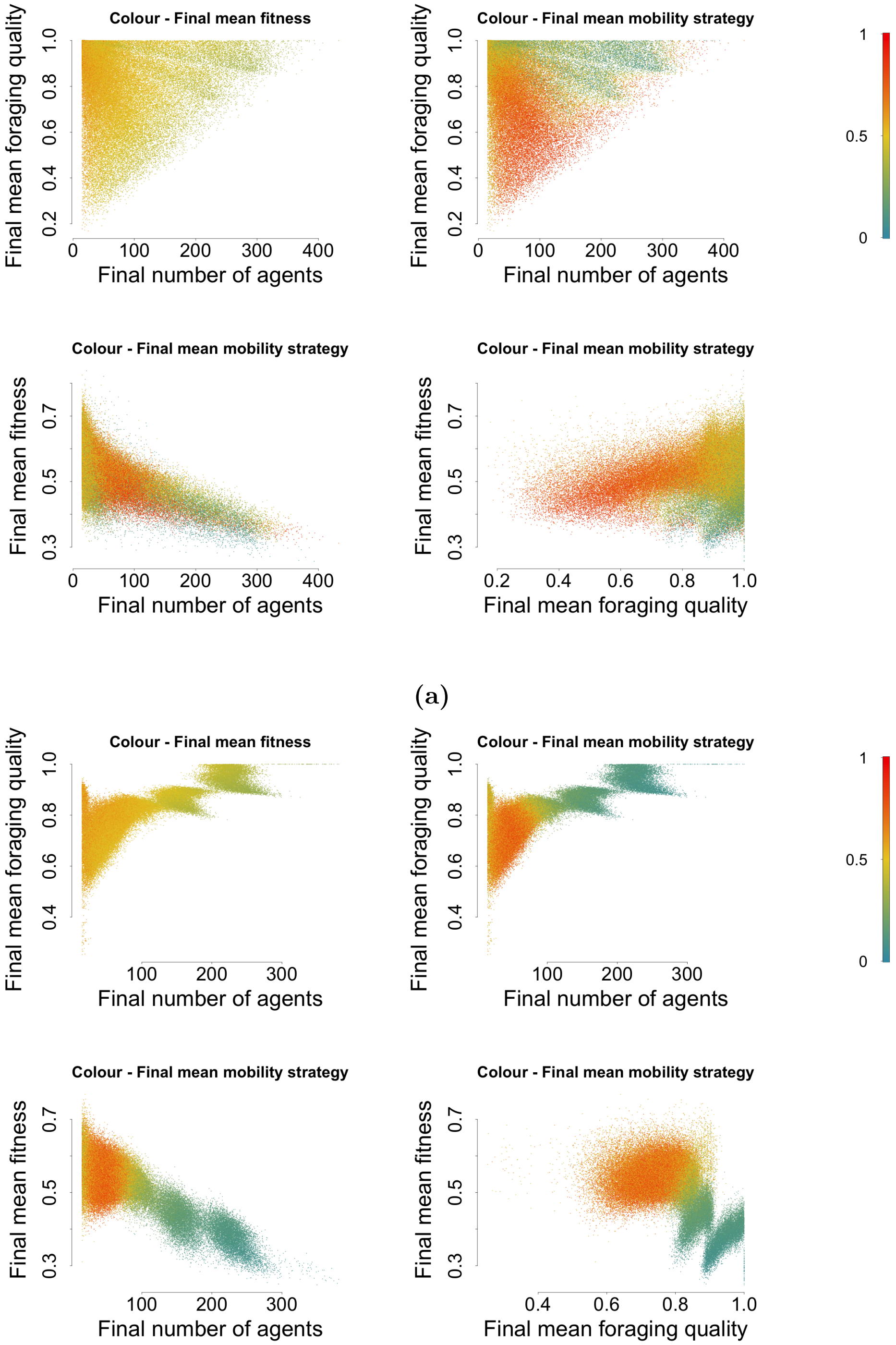
Table 5.5: Pearson product-moment correlation coefficients for every combination of parameters and outcomes in the 98,657 simulations with ≥ 15 agents alive in the final iteration. When two parameters are varied. All correlations $> |0.05|$ are significant (p-value < 0.05).

	r	λ	Initial mean mobility strategy	Initial mean null strategy	Final number of agents	Final mean mobility strategy	Final mean fitness	Final mean null strategy
λ	0.012							
Initial mean mobility strategy	0.003	0.002						
Initial mean null strategy	0.002	-0.005	0					
Final number of agents	0.415	-0.736	-0.002	0.005				
Final mean mobility strategy	-0.256	0.722	0.069	-0.003	-0.85			
Final mean fitness	-0.243	0.64	0.011	-0.002	-0.83	0.722		
Final mean null strategy	0	-0.007	-0.003	0.209	0.006	-0.007	-0.005	
Final mean foraging quality	0.538	-0.534	-0.009	0.002	0.782	-0.731	-0.53	0.002

Outcome Clusters

As when I varied all the parameters, I also used the Outcome Clustering (OC) method (discussed in Section 2.4.4) to find groupings of simulation outcomes in both the simulations where four parameters were varied and when two were varied. For each of the 9 clusters found I plotted the relative density of outcomes and parameters; these are shown in Figure 5.16 and 5.17 for when four and two parameters are varied, respectively. Figures 5.16b and 5.17b show the relationship between outcomes coloured by the cluster the simulation was assigned to, when four and two parameters are varied, respectively. As with when I varied all the parameters, the continuation of outcome types from between State A and State B clusters can still be seen, but when I vary fewer parameters the separation of the clusters become much more defined.

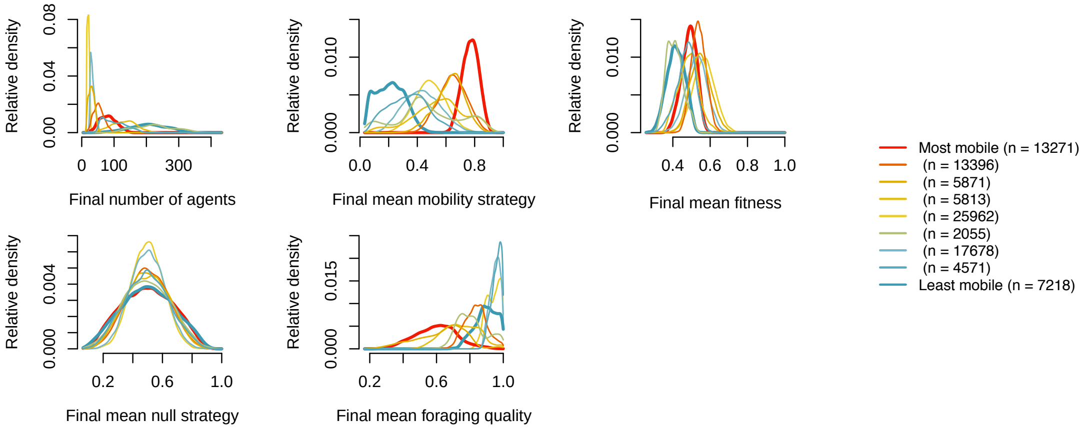
I plotted each parameter pair coloured by the cluster the simulation was assigned to in Figure 5.18. Here it can be seen that the ratio between the growth rate and the depletion rate (r and λ) is strongly correlated with which cluster the simulation belongs to, however, the relationship is not linear – the highest values for r/λ (high r, low λ) give the State B outcomes (the blue cluster), but the lowest values for r/λ (low r, high λ) give the cluster somewhere between State A and State B (a yellow cluster).



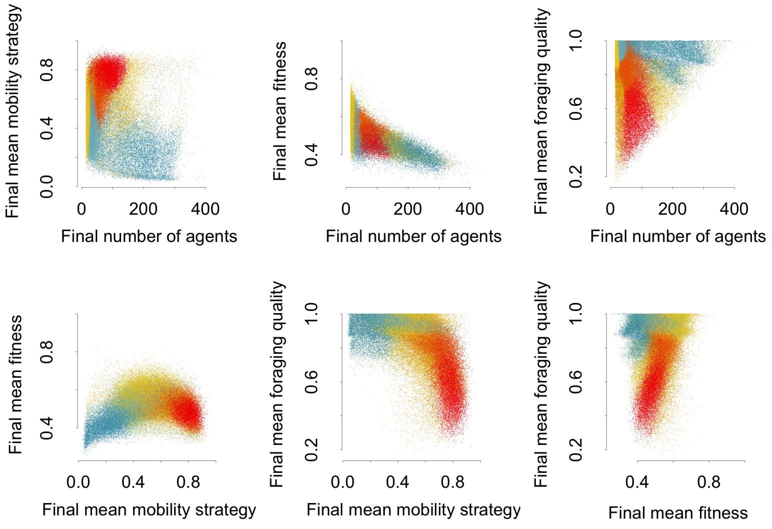
(a)

(b)

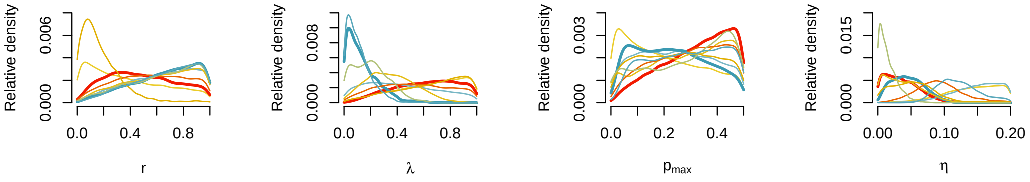
Figure 5.15: 3D representations of 3 outcomes (x and y axis, and colour) in the simulations with $\geq$ 15 agents alive in the final iteration, using simulations where 4 parameters were varied (a) and 2 parameters were varied (b).



(a) Outcomes in different clusters.

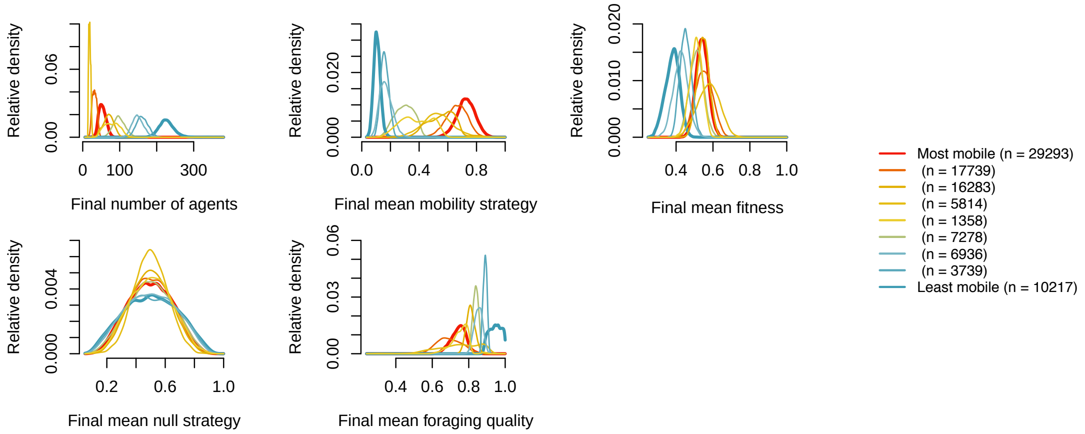


(b) Outcome pairs coloured by cluster.

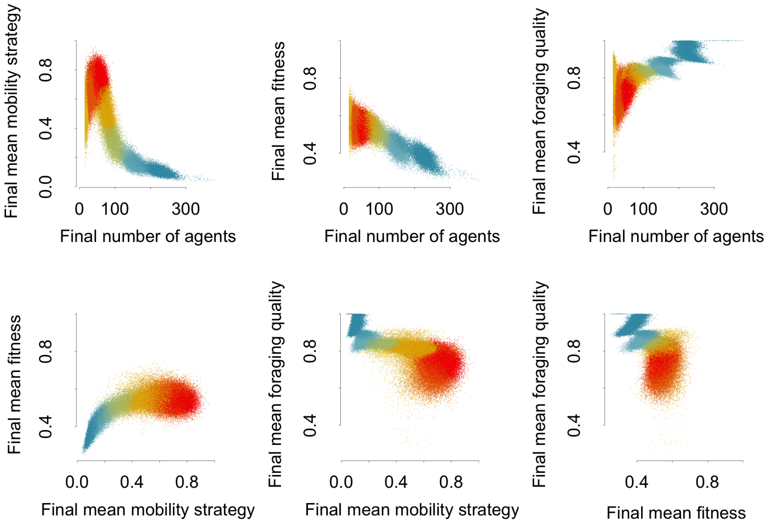


(c) Parameters in different clusters.

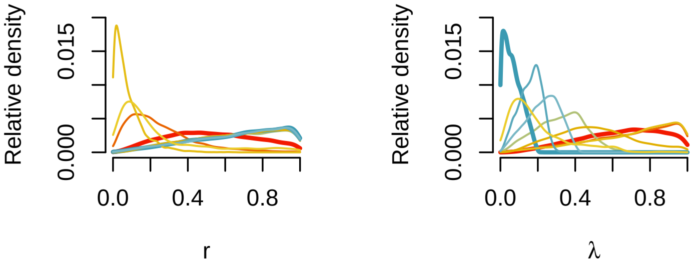
Figure 5.16: The outcomes and parameters in the different clusters, using the 95,835 simulations with ≥ 15 agents alive in the final iteration when four parameters are varied. In the relative density plots the most and least mobile clusters are highlighted with a thicker line.



(a) Outcomes in different clusters.

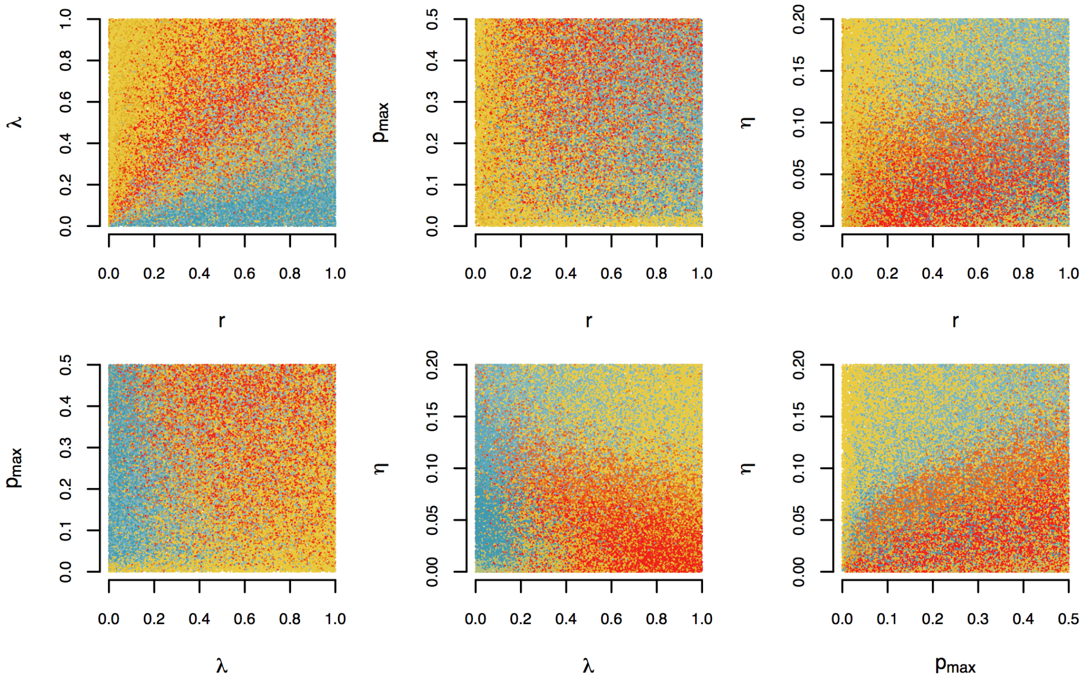


(b) Outcome pairs coloured by cluster.

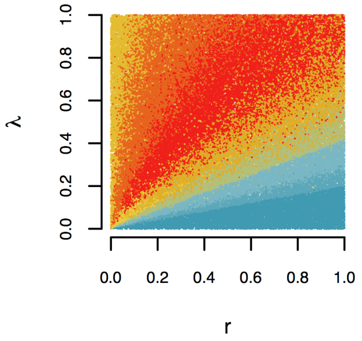


(c) Parameters in different clusters.

Figure 5.17: The outcomes and parameters in the different clusters, using the 98,657 simulations with ≥ 15 agents alive in the final iteration when two parameters are varied. In the relative density plots the most and least mobile clusters are highlighted with a thicker line.



(a) Parameter pair relationships coloured by cluster, when varying four parameters.



(b) The relationship between r and λ coloured by cluster, when varying two parameters.

Figure 5.18: The pairwise relationships between parameters coloured by cluster. For when four parameters are varied (a) and when two parameters are varied (b). Cluster colours are the same as in Figure 5.16 and 5.17.

5.4 Temporal and Spatial Variability

In the previous section I have shown how different parameter combinations can affect the outcomes of my model, but within a simulation the parameter values were constant for each iteration and for every site. In this section I look at both the effects of temporal (changing every iteration) and spatial (changing every site) variability in parameter values. To investigate specifically the effect of temporal and spatial *environmental* variability I only varied the parameters which directly relate to the sites – the growth and depletion rates, r and λ.

5.4.1 Temporal Variability – Experiment 8

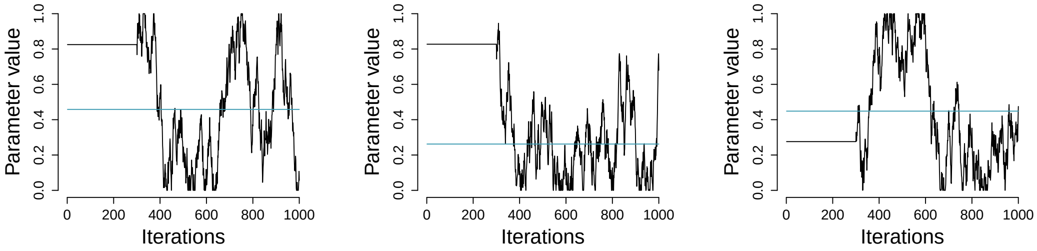


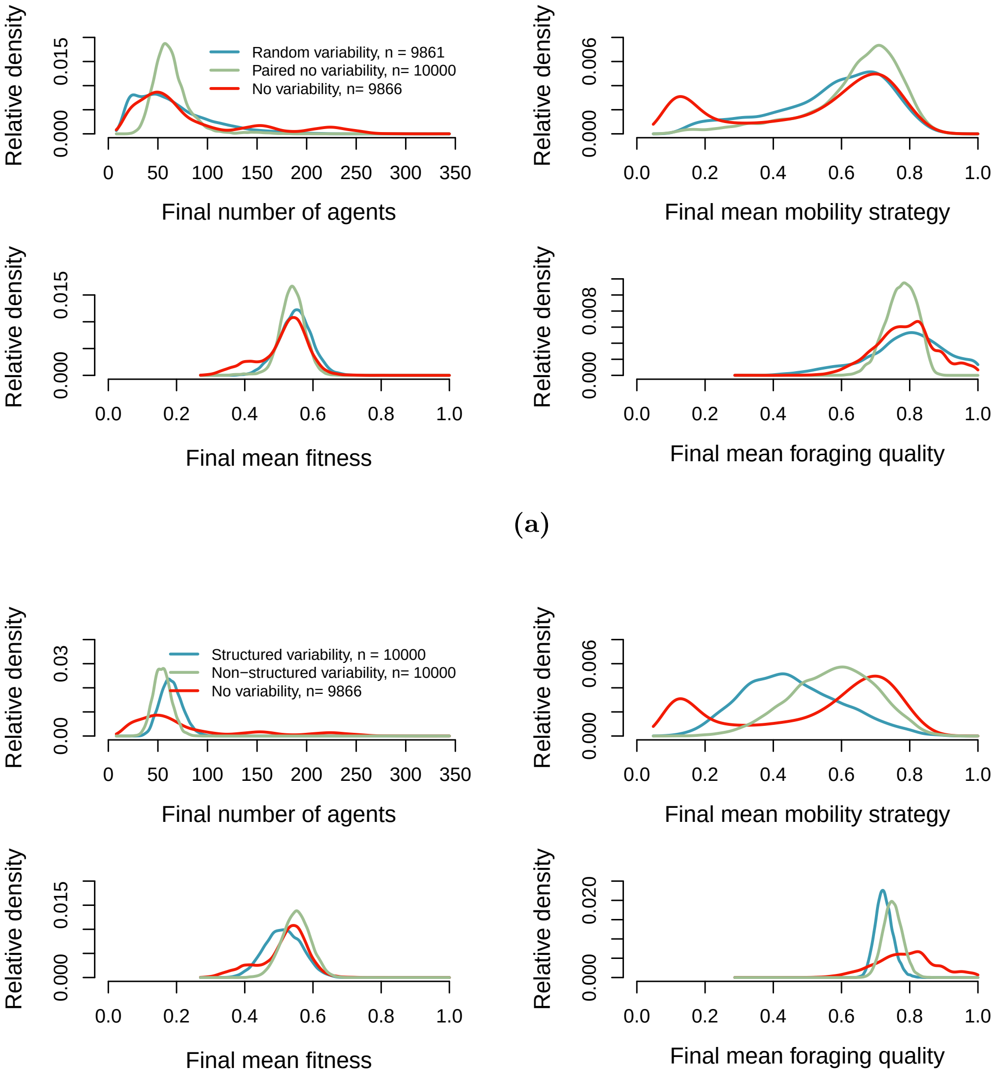
Figure 5.19: How a parameter value changes over time when there is temporal variability in r and λ. The dynamics with three random starting points and a walk distance of 0.1 are shown. The blue line shows the mean parameter value from iteration 300 to 1000.

I ran the model 10,000 times with random values for the growth and depletion rates, r and λ (for details of this run see Table H8). After a run-in period of 300 iterations I then randomly varied r and λ every iteration. This was done according to a random walk, where new values for the parameters were picked randomly in $[\text{previous value} - WD, \text{previous value} + WD]$, where WD is the walk distance. Three randomly generated examples of how a parameter value can change over time using this method can be seen in Figure 5.19.

The average values of r and λ from the iterations in which they were varied (iterations 301 to 1000) were then used in 10,000 simulations without variability (referred to as the 'paired no variability' run). Thus I have 10,000 pairs of simulations, with one simulation with temporal variation in r and λ, and one simulation with the means of these value used throughout the iterations. I also ran 10,000 simulations with a random r and a random λ value chosen for each simulation (as in Experiment 7; the 'no variability' run), for further comparison. I compared the relative frequencies of the simulation outcomes for each of the types of run in Figure 5.20a. This figure shows when there is random variability there are fewer simulations with low mean mobility values. This could be because for low mean mobility strategies to evolve a persistent state is needed. It could also be because to promote low mobility simulations quite specific parameter values are needed (in particular a low λ from what I have shown previously), and when there is random variability these values are unlikely to come up – as shown by the lack of low mobility simulations in the paired no variability run of the model. Hence, it is possible that low mobility is not necessarily directly promoted from no variability, but rather there are more chances of the conditions being good enough for low mobility. It is interesting to note that the modal value (where the peak is) for the higher mobility strategy is the same in all three runs of the model.

I also performed this experiment the opposite way around, where from iterations 1 to 500 there was random variability in r and λ, and from iterations 501 to 1000 the values for r and λ were kept the same. The results from this were almost identical to when there is no temporal variability – see Appendix J.

I ran a further experiment where r and λ randomly changed every iteration according to the random walk described above, but in this case there was no run-in period and I also chose different values for WD (between 0 and 1) in each of the 100,000 simulations (otherwise this experiment is the same as Experiment 8). Varying WD means I can see the entire range from no variability ($WD = 0$) to extreme variability ($WD = 1$). I found that it is only for the simulations with the lowest values of WD (i.e. where there is little variability) that there are the low mobility, high numbers of agents and low fitness (State B) simulations – this is shown in Figure 5.21.



(a)

(b)

Figure 5.20: Relative densities of simulation outcomes when testing the effect of temporal (a) and spatial variability (b) in r and λ.

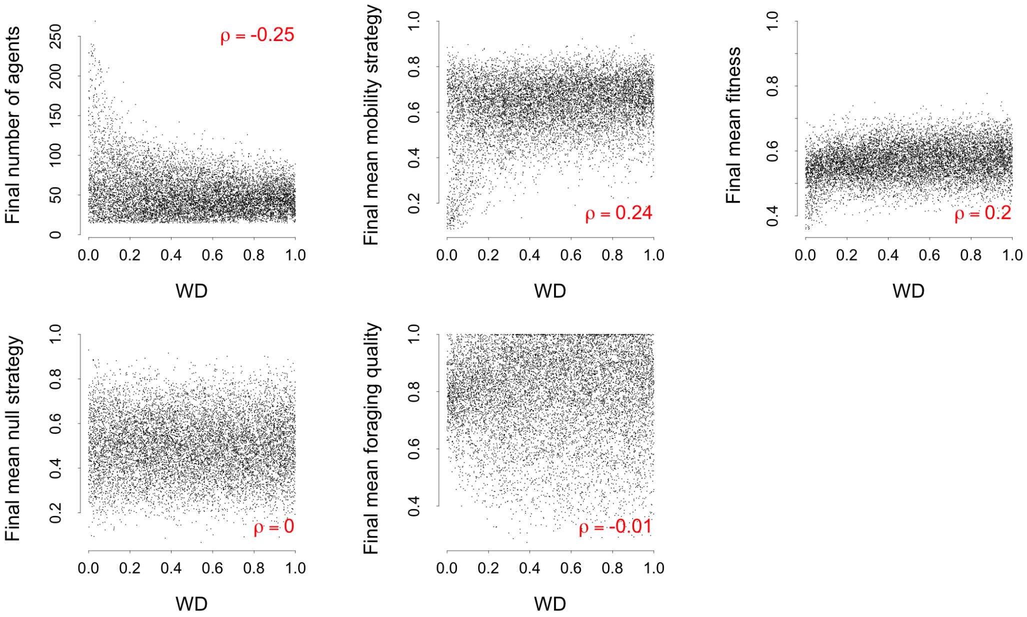


Figure 5.21: Scatter plots of the value randomly chosen for the random walk distance (WD) and outcomes in each of the 9904 simulations with ≤ 15 agents alive in the final iteration. Pearson's rank correlation coefficient, ρ, is given in red.

5.4.2 Spatial Variability – Experiment 9

I also considered the effect of spatial variability in the environmental conditions. I do this by varying r and λ continuously in the x and y direction of the region (i.e. each site has a different combination of values for these two parameters) – this is referred to as 'structured spatial variability'. I compare this to a run where r and λ are randomly picked for each site each simulation (the 'non-structured spatial variability' run), and also a run where only one value for r and λ is chosen each simulation and therefore there is no spatial variability (this is the usual type of condition). An illustration comparing these types of run is shown in Figure 5.22. I run the model 10,000 times over 1000 iterations for all three of these conditions.

I look at the relative frequencies of the parameters and outcomes in the structured and non-structured variability and the no variability environment conditions (as before I only consider the simulations with ≥ 15 agents in the final iteration) in Figure 5.20b. As with temporal variability it seems that it is only when there is no variability that the distribution of mobility strategies is bimodal, with one mode at a particularly low value. However, the modal values are lower in both the structured and non-structured runs of the model as compared to the higher mode in the run with no variability.

I also found the final mean conditions at each site in all 10,000 simulations of the model. For example, for site 1 I look at all the agents at this site in the final iteration of each of the 10,000 simulations, and then take an average of all their mobility strategies. Figures 5.23a and 5.23b show the final mean mobility strategy and the final number of agents at each site for each of the structured and non-structured spatial variability and no variability environment conditions. I found that for the structured spatial variability run the sites are occupied by agents with quite different mobilities and numbers – i.e. there is spatially structuring of the population. The range of mobilities for these sites does not include the highest values, and hence it makes sense that the mean final mobility value was around 0.4 (as seen in Figure 5.20b). When there is non-structured spatial variation I find that all the sites have a mid value for their mean mobility strategy. When there is no spatial variability the values for r and λ will be uniform for the whole region, but these values change every simulation. Hence the final site mean mobilities are all quite similar, but this value will change every simulation. The outer sites are less densely populated than the inner sites when there is no spatial variability, which is an artefact of movement to inner sites being more likely.

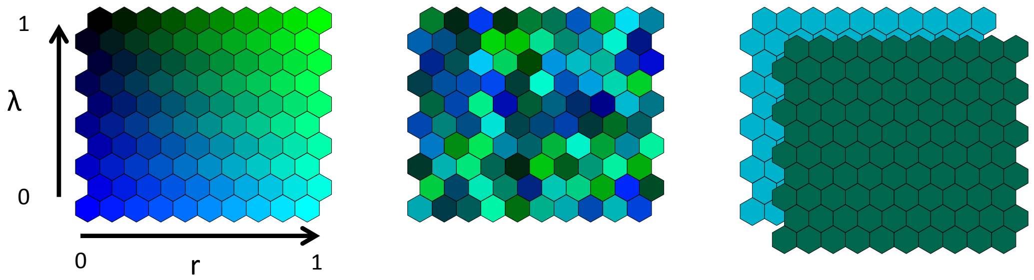
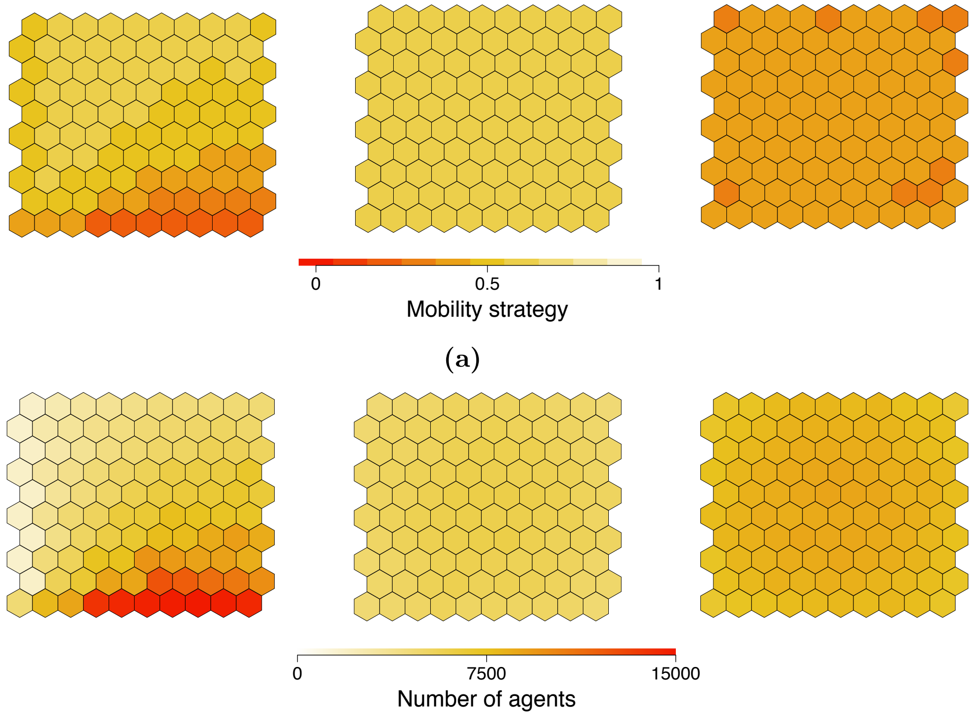


Figure 5.22: Values for r and λ at each site in the structured (left) and non-structured (middle) spatial variability, and no variability (right, where each simulation will have a different value) runs of the model. For the non-structured and non variability runs of the model these values are picked randomly each simulation.



(a)

(b)

Figure 5.23: Final mean mobility strategies (a) and number of agents (b) in each of the structured (left) and non-structured (middle) variability and no variability (right) models runs.

5.5 Model Events Over Time

In Section 5.3 I considered how the parameter values in the model affected the final state of agents and sites. I showed that certain parameter combinations could cause simulations to fall into two states: State A with low numbers of agents, high mobility strategies, high fitnesses and low foraging quality, and State B with the opposite qualities. In this section I will consider the model dynamics over time, and also try to understand the processes which could lead foragers to switch from State A to State B. In particular I want to find if there is an order in which the simulation qualities change, e.g. does the number agents start to increase before the mean mobility decreases or vice versa?

Previously the initial agents of the model had mobility strategies between 0.01 and 0.99, but the simulations discussed in this section started with all the agents being highly mobile – I chose the initial mobilities to be between 0.8 and 0.99. I also did this for the null strategy. I ran 1000 simulations of the model with different values for r and λ, and the other parameters were at their default values, see Table H10 in the Appendix.

5.5.1 Dynamics Over Time – Experiment 10

The number of agents and the mean mobility strategies, fitness, null strategies and foraging quality are shown over all iterations for each of the 1000 simulations in Figure 5.24 (coloured by final mean mobility) and in Figure 5.25 (coloured by the the ratio r/λ). These dynamics can be seen in closer detail for the first 20 iterations in Figure 5.26. As mentioned at the beginning of this chapter, model outcomes are recorded at the end of each iteration, and hence even though initially there are always 60 agents, the plots show at iteration 0 the number of agents is roughly between 40 and 60.

As can be seen from Figure 5.24, the simulations which change most over time (for all outcomes) are those with the lowest final mean mobilities. By comparing the mean null strategies over time to the mean mobility, I find that random drift will somewhat lower the strategies over time, but there are distinct simulations for which the mean mobility strategy becomes significantly lower.

In general, regardless of the ratio of r and λ, the mean foraging quality will almost immediately increase to a steady value (see the mean foraging quality plot of Figure 5.25). For simulations where $r > \lambda$ this steady value will be higher than when $\lambda > r$, which is intuitive since the foraging quality is growing faster and there is less depletion. The value for r/λ seems to predict, as in Section 5.3, whether the simulation is going to

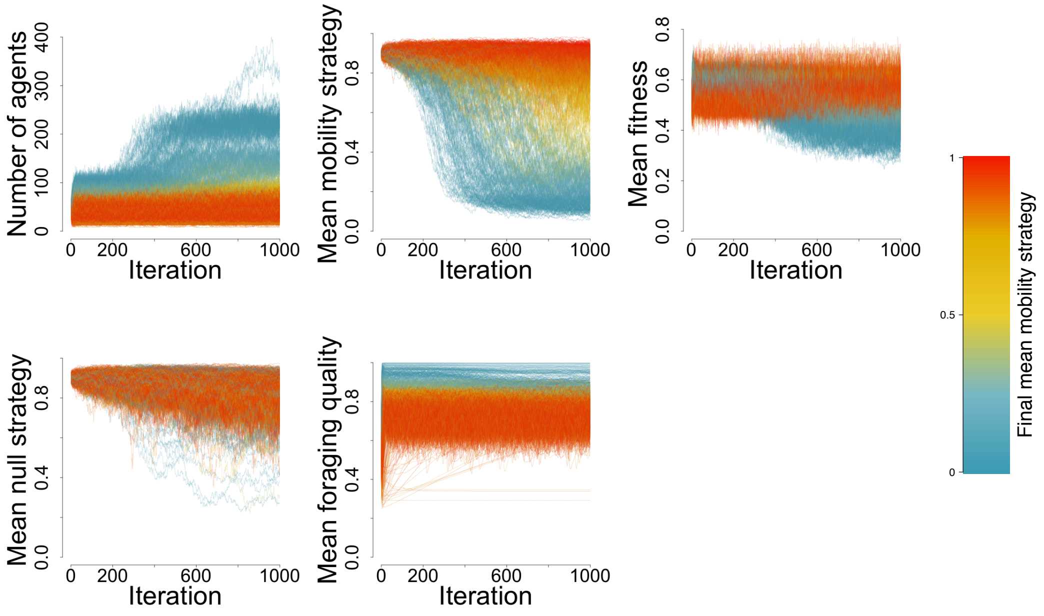


Figure 5.24: Simulation properties at each iteration coloured by the final mean mobility strategy.

have a low final mean mobility (and high number of agents and lower final mean fitness); however, there does seem to be a discrepancy in the highest values for r/λ where the simulations do not have the lowest final mean mobilities or have the least final mean fitness.

When there is no effect from depletion ($\lambda = 0$) the simulations are quite different to the others – they have the highest number of agents, and the lowest mean mobility and fitness, but take more iterations before they start to change (the three simulations for which $\lambda = 0$ are shown in black in Figure 5.25). This could be because selection to become sedentary is slower, since fewer agents will be dying due to the foraging quality being good even if the site is occupied by many agents. In three of the simulations for which $r = 0$ all the agents died in the first 21 iterations.

It is apparent that the simulations have 'settling in' dynamics – where in the first few iterations the short-term behaviour is slightly different until it has chance to stabilise into the long term behaviour (seen in Figure 5.26). In these first few iterations there is a decrease in the number of agents followed by an increase in fitness.

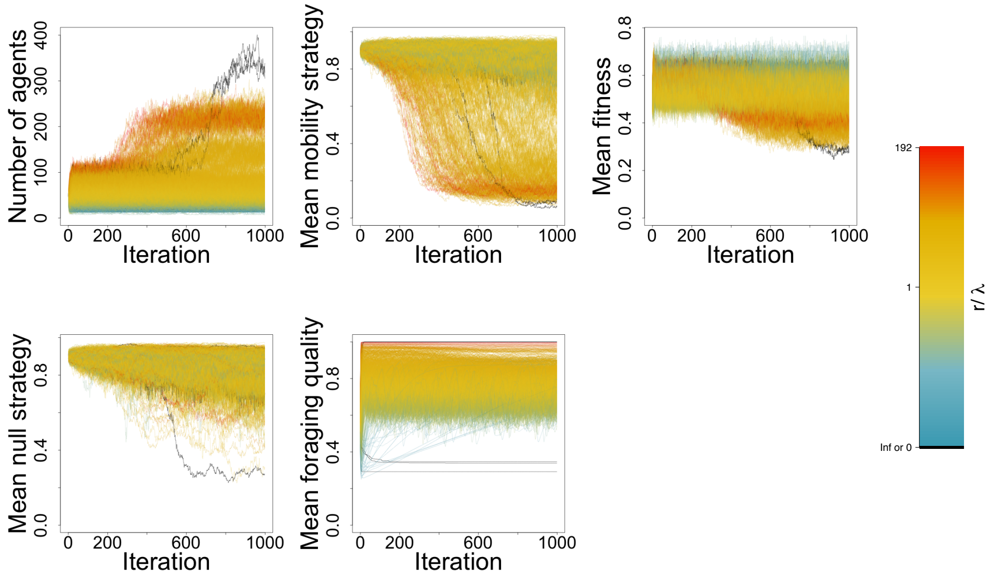


Figure 5.25: Simulation properties at each iteration coloured by the ratio of the parameters r and λ. Black represents when $r = 0$ or $\lambda = 0$. Colours are log scaled.

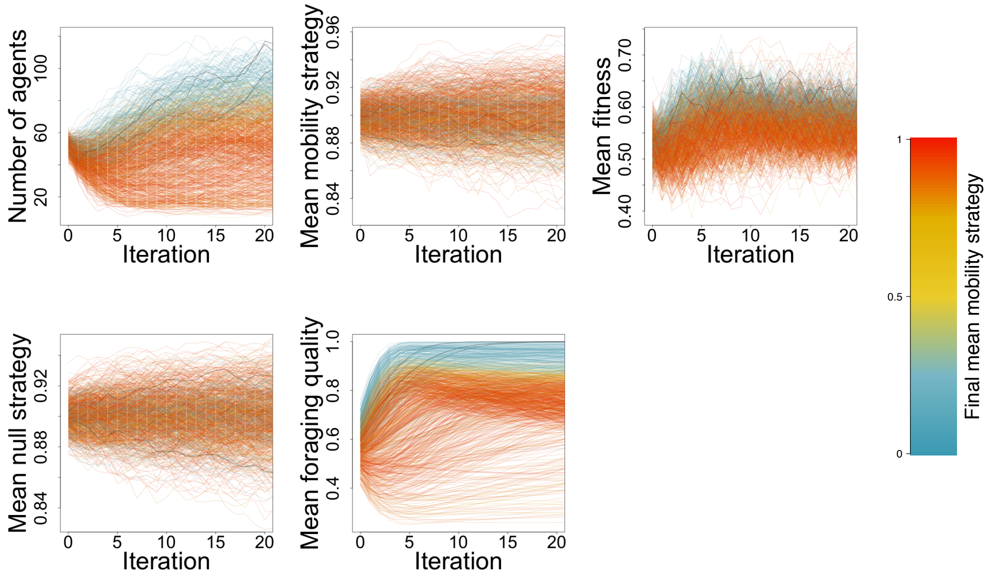


Figure 5.26: Simulation properties in the first 20 iterations coloured by the final mean mobility strategy. The three simulations where $\lambda = 0$ are shown in black.

5.5.2 Ordering Model Events

Out of the 1000 simulations 234 had a final mean mobility strategy of < 0.5. 30 of these simulations are shown in Figure 5.27, where the mean mobility, fitness, and number of agents are plotted. By using the algorithm in Section 2.4.2 I was able to predict the point at which there is a significant change in the number of agents, the mean mobility and mean fitness. This algorithm fits linear models to the outcomes in consecutive blocks of iterations (e.g. the mean effort strategy from the first 100 iterations), and finds the point at which the gradient significantly changes. Applying this algorithm allows me to quantify whether the decrease in mean mobility strategy started to happen before or after the increase in the number of agents. By looking at the points of change predictions using different block sizes by eye, I found that a block size of 140 is suitable. Since the number of agents always slightly increases in the first iterations of the model, I decided to not include the transition between iterations 1 to 140 and iterations 141 to 280 as the point of change when considering the number of agents.

I estimated that of the 234 simulations where the mean mobility decreased to < 0.5, 212 had a decrease in mobility before an increase in the number of agents, 1 had the opposite, and 21 had them happen at the same time. Due to how the algorithm works I can only predict the time of change to the nearest 140 iterations. The time these changes occurred is shown in Figure 5.28. Table 5.6 gives the number of times each of the different orders for simulation changes occurred when the mean fitness is also considered, in the 212 simulations where significant changes in mobility occurred before significant changes in the number of agents. The most common order of events is when the mean mobility decreases first, and then the number of agents increases and the mean fitness decreases. It is rarely the case that the mean fitness decreases before the mean mobility decreases.

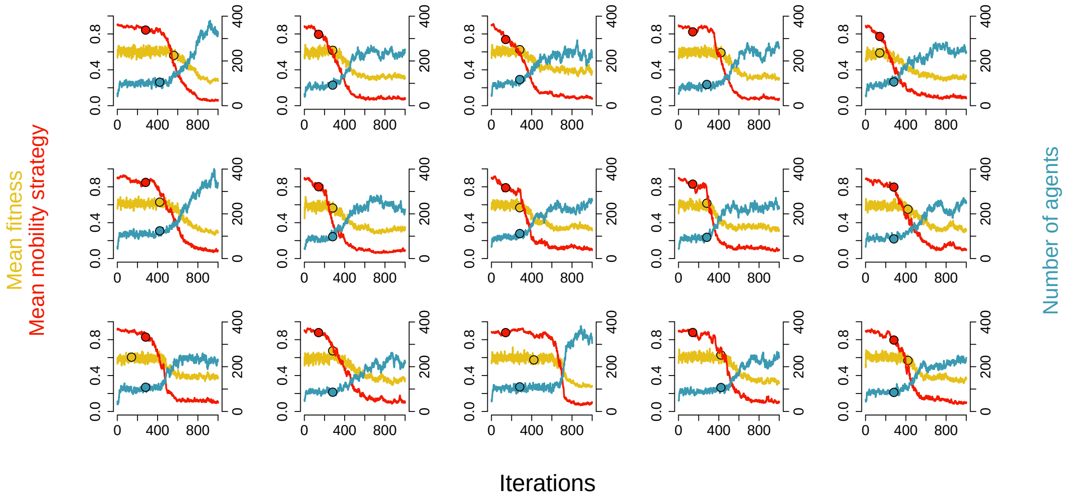


Figure 5.27: The dynamics of 15 simulations from the 234 simulations where the final mean mobility strategy was < 0.5. Red shows the mean mobility strategy over time (left y-axis), yellow shows the mean fitness over time (also left y-axis), and blue shows the number of agents over time (right y-axis). Circles show where my algorithm identifies a significant change in gradient to occur.

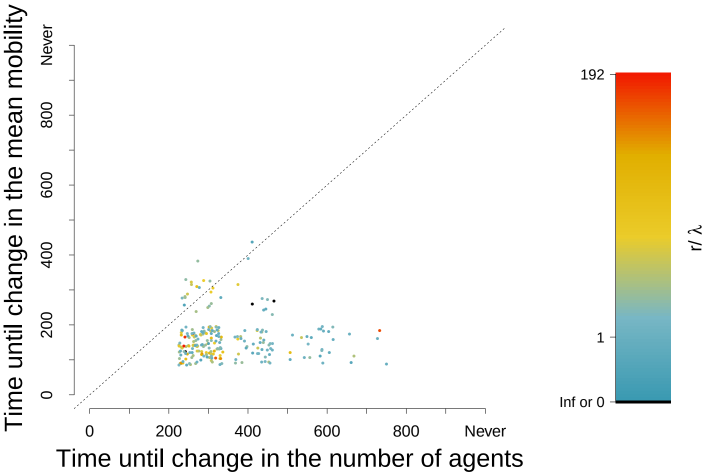


Figure 5.28: The number of iterations until there was a change in the number of agents as compared to when there was a change in the mean mobility strategy, in the 234 simulations where the final mean mobility strategy was < 0.5. The dashed line shows where these are equal. Coloured by r/λ (log scaled).

Table 5.6: How many times each of the different orders for simulation changes occurred. Only using the 212 simulations where a change in mobility happened before a change in the number of agents, and when the final mean mobility was < 0.5. I abbreviate the mean mobility as $\bar{m}$, the number of agents as N, and the mean fitness as $\bar{f}$. E.g. $\bar{m}$ then N then $\bar{f}$ – how many times mean mobility decreases then the number of agents increases and then the mean fitness decreases.

Order	Number of simulations
$\bar{m}$ then N and $\bar{f}$	79
$\bar{m}$ and $\bar{f}$, then N	63
$\bar{m}$ then N then $\bar{f}$	50
$\bar{m}$ then $\bar{f}$ then N	17
$\bar{f}$ then $\bar{m}$ then N	3

5.6 Discussion

In this chapter I have explored the model described in Chapter 4. This has involved running many simulations to understand model behaviours and outcomes, thoroughly exploring parameter sensitivity, and running various experiments to test the effect of environmental variability. The work has allowed me to make predictions about the reasons for variability in hunter-gatherer mobility as well as allowing me to understand the workings of the model before adding more complexity (which I will do in the next chapter).

In this section I will discuss and suggest limitations of the results presented in this chapter.

5.6.1 Parameter Sensitivity and Simulation Outcomes

My analysis from Section 5.3 involved running the model many times using different parameter value combinations. This allowed me to properly consider the interdependencies of the model, and find which parameters influenced certain outcomes.

Outcomes Interdependencies

Using the correlation coefficients given in Table 5.3 I find that there are correlations with $|\rho| > 0.15$ between the final number of agents, the final mean fitness, and the final mean foraging quality. These make intuitive sense: a higher foraging quality means there is more to eat and so fitness will be higher; higher fitness means the probability of birth is higher so there can be more agents, but on the other hand more agents mean there are more people to share the foraging quality with, resulting in lower fitness; and higher numbers of agents mean there will be more impact from depletion, so the foraging quality will be smaller (these relationships can be further understood using Equations 4.1, 4.2 and 4.8).

There are also some moderate correlations ($\rho \approx 0.4$) between the final mean mobility strategy and both the final mean fitness and the final mean foraging quality. The implications of these observations are not so intuitive since there is no implicit relationship between mobility and other aspects of the model (i.e. there are no equations involving an agent's mobility strategy), and hence the effects are indirect and multi-factored. Since there is a fitness cost to movement, one may expect mobility to be negatively correlated with fitness; however it is positively correlated. Furthermore, since staying at one site for number of iteration incurs a depletion cost to the site, it may also be expected that mobility would be positively correlated with foraging quality, but I find it is negatively correlated. Hence, there are obviously some indirect mechanisms which influence the final mean mobility strategy. Since the number of agents is highly correlated with these outcomes, it is likely that this plays a part in these apparent contradictions.

As I increase the number of parameters I fix (from fixing none, to 4 to 6) I find that these relationships still hold, but the correlations become stronger, probably because reducing parameter variability reduces noise. I also find a correlation between the final number of agents and the final mean mobility strategy.

Simulation Types

My clustering analysis revealed different outcome groupings. In general these were a continuum between having high mean mobility strategies, high mean fitness, low numbers of agents and low mean foraging qualities; and having low mean mobility strategies, low mean fitness, high numbers of agents and high mean foraging qualities. I referred to these outcomes types as State A and State B respectively. As I decreased the number of parameters varied the values for these two types of outcomes overlapped much less. As I showed from my review of Kelly's (2013) hunter-gatherer mobility data in Section 2.5.1, the exponentially decreasing relationship between reduced mobility and larger population density (seen in Figure 5.16b) is also seen in real populations.

There were other clusters found with qualities in between the State A and B clusters, but there were some clusters where the mean mobility strategies were around 0.5 but the number of agents was much lower than those in the State A clusters. These simulations are also those with the lowest growth rates, and I suspect that if given more time all the agents in these simulations may have died.

Parameter Sensitivity

When I varied all of the parameters I found 3.1% of the simulations had no agents alive in the final iteration. These simulations had low values for the maximum number of agents that could live at site, and initially had low population density – which can be seen from Figure 5.7. These conditions mean that there will be fewer agents in the population – which can be good because foraging quality is shared between fewer agents (so fitnesses are higher), and there will be less of a depletion impact (so the foraging quality will be better). However, fewer agents can also mean there is less of a buffer if agents do die, so the population's survival is more fragile. Hence, even though foraging quality and fitnesses will be higher, low numbers of agents will still pay the cost of movement, and if this is not too low (which is also seen in Figure 5.7) it could mean that some of the already small numbers of agents die and the population never recovers.

In the simulations where there were ≥ 15 agents alive in the final iteration there were many strong correlations between various pairs of parameters and outcomes (given in Tables 5.3, 5.4 and 5.5). Since there are also correlations between pairs of outcomes it is difficult to ascertain which parameter values directly affected simulation outcomes. However from my clustering analysis I can see which parameter values are in the different types of simulation clusters, which are shown in Figures 5.13, 5.16c and 5.17c.

In none of the clusters was there a preferred value for κ_m or μ and thus mutation of strategies seems to play little part in whether a simulation evolves into a particular cluster type (which was confirmed in Appendix I when I set $\mu = 0$). Hence when frequencies of strategies change in the population it is because agents with certain strategy values are more likely to die, and/or agents with other strategy values are more likely to fission. Strategy frequencies do not change because of the random nature of mutation, and thus the final mean strategy value is resistant to the introduction of new strategies – in other words the final strategies are evolutionary stable strategies (as defined in Maynard Smith, 1972).

The maximum number of agents, n_{max}, that a site can support was influential on which cluster a simulation was in. I found that State A clusters had low values, but not too low (although when n_{max} is too low all the agents can die, and therefore the simulation would not have been included in the cluster analysis), and State B clusters had high values for n_{max}. If n_{max} is high, then there is the potential for a large number of agents (as long as the foraging quality is not too low), and if this occurs decreased mobility may be selected for since there would be little benefit in paying the cost of movement only to go to a site occupied by many agents. Thus, I predict that when there is decreased mobility there is more homogeneity of sites (in terms of numbers of agents and foraging quality).

The initial density of agents, ρ_{init}, also has an impact on which cluster the simulation is categorised into. I find that State A clusters have lower initial densities, and State B clusters have higher initial densities. A high initial density will promote a large number of agents, and as with my argument for n_{max} this could mean selection for reduced mobility. On the other hand, I find that the values for the upper probability for fissioning, p_{max}, are generally higher in State A outcomes, so although these simulations have the potential to have large numbers of agents (depending on the fitness of agents, see Equation 4.8) they actually have high mobility.

Since the probability of fissioning is a function of both p_{max} and agent fitness, having a high value for p_{max} does not necessarily mean that there is more fissioning. The discrepancy between the preferred value for p_{max} in State A and B outcomes may be to do with how the mobility strategy evolves – in State A outcomes where the values for p_{max} and fitness are generally high, evolution may be facilitated by the birth of more agents with high mobilities; whereas in State B outcomes where the values for p_{max} and fitness can be low, evolution might be also caused by the death of those agents with high mobilities.

In both State A and B outcomes the value for the cost of movement, η, is small. In some ways this will be because even for State B outcomes there is still some mobility, and thus if the cost of movement is too high then all the agents may die, and hence not be included in the analysis. Obviously when the cost is as low as possible then the benefits to being highly mobile are greater, and thus the values for η are lowest in the highly mobile simulations.

State B outcomes generally have the highest values for r and the lowest for λ. Hence for the evolution of reduced mobility it is important for the environmental quality to be high, a result which is also seen from Kelly's hunter-gatherer data (2013) (as discussed in Section 2.5.1) where there is less mobility in areas where there is more to eat. The opposite is not quite true in my model – for State A outcomes r is never too low and λ is never too high; this is because if the values chosen make the the environmental quality too low then all the agents will die. It also appears that it is less important for the value for r to be *not* high, than it is important for the value for λ do be *not* low for State A outcomes (seen by a more spread distribution of values for r). Hence when depletion is a factor and environmental quality is low, mobility is beneficial.

5.6.2 Variability

In my analysis I also investigated the effects of both temporal and spatial variability in the growth and depletion rates. Since these parameters directly affect the foraging quality, I think of their ratio being a measure of environmental quality.

I found that when there is little temporal variability (measured by the walk distance in the random walk, see Figure 5.21) there is more of a spread in the final mean mobility strategies of the simulations, including low mobility strategies. When the amount of temporal variability increased I saw less of these low final mean mobility strategy simulations. Hence, my analysis shows that variability of the environment over time is unfavourable for reduced mobility.

For structured spatial variability I found that there were fewer simulations with either a high or low final mean mobility strategy, and more with a value in between. I also found that the strategies in the population became spatial structured. Hence, rather than simulations either having a majority of agents with high mobility strategies or having low strategies, when there is spatial variability highly mobile and less mobile agents cohabit the region. In comparison, the simulations in the unstructured spatial variability run have higher final mean mobility strategies, even though these have the same sites (just in a random order). Hence, it seems that spatial variability gives mixed final strategies in the population, and if the variability is structured there can be more agents with lower mobility strategies. This could be explained by Kelly's domino effect to switching to sedentism (2013, p. 107) (mentioned in Section 1.4). In this, if clusters of sites are occupied by lots of less mobile agents, then the mobile agents near these sites have less options of sites to go to and are therefore at a disadvantage. And so, there may be some selection pressure for the surrounding sites to be occupied by less mobile agents. When the spatial variability is unstructured, there will be more movement options, since mobile agents only need to avoid single sites isolated around the region, rather than a whole corner of the region.

5.6.3 Events Over Time and Their Order

In Section 5.5 I specifically looked at the processes involved in the evolution of simulations with high mobility strategies to State B outcomes. I showed that simulations have four main stages in their changes over time. The first is a settling-in period of around 20 iterations where the mean foraging quality, which is initially random, is recalibrated to a value predominately determined by the values of r and λ. This change is accompanied in general by a small decrease and then an increase in both the number of agents and the mean fitness. The values are then steady for a period of time after this (approximately for an additional 100 iterations), and then in the simulations with high values for r/λ the number of agents start to increase, and the mean mobility strategy and mean fitness start to decrease. The values then become steady again.

Of the approximately 25% of simulations which had a final mean mobility strategy of < 0.5 I found that it is almost always the mean mobility strategy which starts to decrease significantly before increases in the numbers of agents and reduction in fitness occur. Therefore, there is perhaps a case that lower mobility causes the number of agents to increase and the fitness to decrease. This could be explained by lower mobility (or the conditions which lead to lower mobility) meaning that more agents can survive with low fitness – and thus the average is lowered. In comparison to areas of high mobility, agents may have less of a buffer against bad conditions and thus only those with the highest fitnesses can survive.

5.7 Conclusion

In this chapter I have explored the behaviours, outcomes and parameter sensitivities of the Forager Model. I have seen the interdependencies of parameter values which cause certain outcomes, and how simulation outcomes are clustered into two main groupings. I have also seen how variability affects the results, and how the model changes over time.

In Section 5.3 I showed how simulations generally fall into two categories; one with high mean mobility strategies, high mean fitness, low numbers of agents and low mean foraging qualities; and one with low mean mobility strategies, low mean fitness, high numbers of agents and high mean foraging qualities. I showed how certain parameter values can influence which of these outcomes types the simulations fall in to.

I found that the effects of mutation are insignificant in the model's behaviour over time. I also found that higher values for the maximum number of agents at a site and the initial population density promoted reduced mobility. I hypothesised that these values promote larger numbers of agents, meaning that the probability of moving to a relatively undepleted site is low, and hence there is little point to being highly mobile and paying the cost of mobility. I found that the values for the upper probability of fission are higher in the highly mobile simulations, but in the reduced mobility simulations the values cover a larger range of values. Since lower mobility simulations also have lower fitnesses, I hypothesised that the evolution of low mean mobilities is facilitated more by the death of mobile agents, rather than the fissioning of less mobile agents. I also found that the ratio between the growth and depletion rates is a large factor in which outcome type a simulation has, where for reduced mobility to occur the growth rate should be high and the depletion rate should be small.

In Section 5.4 I showed how temporal variability of the environment was unfavourable for reduced mobility. Spatial variability on the other hand, did not discourage reduced mobility, but rather allowed a region to be cohabited by both highly mobile and less mobile agents. I also found that structured spatial variability allowed for more reduced mobility than non-structured spatial variability.

Finally in Section 5.5 I showed how when there is reduced mobility over time, it is often the reduction in mobility which occurs first, and then the increase in the number of agents and the decrease in the mean fitness.

My model has replicated the known relationships between reduced mobility and high population density, between reduced mobility and higher environmental quality, and between reduced mobility and reduced fitness, seen in hunter-gatherer groups (Kelly, 2013). And although I cannot provide an intuitive explanation for all of the model behaviours, this chapter provides a thorough exploration of the model – a useful basis for the results of the next chapter where the ability for agents to have different subsistence strategies is added.

6

Mobility and Subsistence Strategy Changes in a Mixed Population

Summary

The model described in Chapter 4 looked at the movement of foragers around a region, where environmental conditions were varied. I found that high mobility was linked with low population size and high fitness, whereas reduced mobility was associated with high population sizes and low fitness. In Section 1.1 I discussed how the switch from a foraging to a farming subsistence strategy was linked with reduced mobility, increased population size and environmental changes. Thus, in this chapter I will expand on the Forager Model by allowing agents to have different subsistence strategies.

In the first section of this chapter I will discuss all the changes made to the model to incorporate subsistence strategies. These changes include a new agent strategy and a new site quality measure.

Sections 6.2, 6.3 and 6.4 of this chapter contain both the methods and results of various experiments in running the model. In Section 6.2 I use the FIO method to look at the types of outcomes and the relationships between parameters and outcomes when running the model when all parameters are varied, and also when just the four environmental parameters are varied. The results from this analysis show that the model replicates the relationship between increased population size, sedentism and low fitness in farming populations. I find that sedentary farming occurs in good foraging and farming environments, sedentary foraging occurs in the best foraging but worst farming environments, mobile farming occurs in the worst foraging but best farming conditions, and mobile foraging occurs in bad foraging and farming conditions. Strategy

conservatism makes little difference to the evolution of various strategies, and mutation rate should not be extremely low, but otherwise its value does not have an effect. For the evolution of sedentary farming there should be the potential for high numbers of farmers.

After this, in Section 6.3 I investigate the effect of temporal and spatial environmental variability, and show that these discourage the evolution of sedentary farming, although it can still occur. In Section 6.4 I looked at how the simulations change over time, and find that sedentary farming evolves via either mobile foragers becoming sedentary first or becoming farmers first; farming and sedentism do not occur at the same time. The results from these three sections are discussed in Section 6.5.

6.1 The Forager-Farmer Model

Allowing the ability for agents to farm introduces major changes to the model. These include adding a new agent strategy – the effort strategy, e; a new site quality – the quality of farming, q_a; and various changes to the site quality and agent fitness equations.

In this section I will discuss the changes made to the model described in Chapter 4. All the model constants, variables and parameters are summarised in Table 6.2 and an overview of the model is given in the flow diagram on page 201.

6.1.1 Effort Strategy

Agents will now have an 'effort' strategy, e, which is how their effort (which can be thought of as labour and or time) is divided between farming and foraging when procuring subsistence. This is similar as in the models of Baker (2008) and Dow et al. (2009), discussed in Section 2.3. In contrast to the model of Bowles and Choi (2013) the subsistence strategies of agents are continuous. Thus, an agent may have an effort strategy of 0.3, which would mean 30% of its subsistence effort is spent foraging and 70% is spent farming. In a model with only foragers (as in the Forager Model) all agents would therefore have $e = 1$.

This strategy can change over time with the same mechanisms as the mobility strategy. Namely, when an agent fissions it passes on its effort (and mobility and null) strategy to the new family. Also, with a probability of μ the agent will mutate its effort (and mobility and null) strategy. If this happens the mutated strategy value will be picked from the Binomial distribution

$$B(n^*, p^*) = B(\kappa_e f, e_0) \tag{6.1}$$

and then divided by $\kappa_e f$, where e_0 is the agent's original effort strategy value, f is the agent's fitness, and κ_e is the degree of effort strategy conservatism (equivalent to κ_m). As with the mobility strategy, the effort strategy needs to be not equal to 0 or 1, hence I take $e \in [\,0.01, 0.99\,]$.

6.1.2 Foraging and Farming Fitness Effects

In the right environment, farming can support more people than foraging can (as seen in evidence of the NDT, Bocquet-Appel, 2011b). I include this in my model by assuming that the fitness possible from the best foraging quality is less than or equal to that for the best farming quality. Thus farmers have the potential to fission more than foragers since their fitnesses can be higher. I introduce the parameter, ϕ, to scale the quality of farming with relation to foraging.

In the previous model, where agent fitness is q_f/n, only one forager ($e = 1$) can have maximum fitness ($f = 1$) when $q_f = 1$. When farming is added to the model I assume that $\leq \phi$ farmers ($e = 0$) can have maximum fitness when $q_a = 1$. Hence, ϕ times more farmers can be supported than foragers.

Using the data from Bocquet-Appel (2011b) I showed in Section 2.5.2 that a maximum of around 4.2 times more people could be supported after farming began in comparison to before farming began. Since this needs to be an integer value, I will take $\phi = 5$ as an estimated default value.

6.1.3 Agent Yield and Fitness

Since the fitness of agents can now be influenced by both farming and foraging, I include the concept of 'yield' to distinguish between these contributions. The fitness of the agent is simply the sum of the yields from both of these activities, $Y_f + Y_a$, where Y_f is the foraging yield and Y_a is the farming yield.

In the Forager Model the fitness of an agent at a particular site was simply the foraging quality divided by the number of agents at the site. Since the occupants of a site may now all have different strategies, I want an agent's share of the foraging and farming qualities of the site to be scaled by its effort strategy. Hence, the qualities of the site are shared between the agents living at the site proportionally to every agent's effort strategies – this is illustrated in Figure 6.1. For example an agent with $e = 0.3$ will take less of a share of the foraging quality, but a higher share of the farming quality, than an agent with $e = 0.9$.

The foraging and farming yields for an agent with an effort strategy of e_k are

$$Y_f = \begin{cases} \frac{e_k}{\sum_{i=1}^{n} e_i} q_f, & \text{if } \sum_{i=1}^{n} e_i > 1 \\ e_k q_f, & \text{otherwise} \end{cases} \tag{6.2}$$

and

$$Y_a = \begin{cases} \frac{(1-e_k)}{\sum_{i=1}^{n}(1-e_i)} q_a \phi, & \text{if } \sum_{i=1}^{n}(1-e_i) > \phi \\ (1-e_k) q_a, & \text{otherwise} \end{cases} \tag{6.3}$$

where $\sum_{i=1}^{n} e_i$ is the sum of all the effort strategies of the n agents occupying this site.

Note that these equations are consistent with the previous model. In this every agent was a forager (i.e. all the effort strategies would be 1), and hence $\sum_{i=1}^{n} e_i = n$ at every occupied site. Thus the foraging yield would be

$$Y_f = \begin{cases} \frac{q_f}{n}, & \text{if } n > 1 \\ q_f, & \text{if } n \leq 1. \end{cases} \tag{6.4}$$

At an occupied site $n \geq 1$ holds, thus for both cases we have it that $Y_f = q_f/n$. Since there is no farming in the previous model the farming yield is 0, and hence agent fitness is indeed q_f/n.

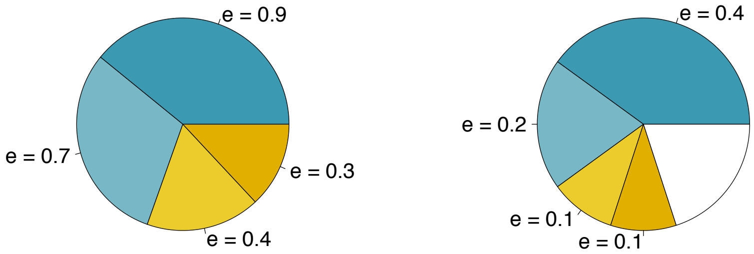


Figure 6.1: Examples of foraging yield. How the foraging quality, $q_f = 1$, is shared between four agents with different effort strategies. On the left $\sum e > 1$ and on the right $\sum e < 1$.

6.1.4 Site Quality

Farming requires land clearance, and therefore will impact on the natural resources of an environment. Therefore in my model the quality of foraging will be impacted by the amount of farming, and thus Equation 4.1 becomes

$$q_{f,t+1} = q_{f,t} + rq_{f,t}(1 - \frac{q_{f,t}}{1}) - \lambda(1 - \frac{1}{n+1}) \sum Y_f - \beta \sum Y_a, \tag{6.5}$$

where β (the farming interference parameter) scales the negative impact from the amount of farming. Note that this is the same as the equation for q_f (Equation 4.1) in the previous model, since when there are only foragers $\sum Y_f = q_f$ and $\sum Y_a = 0$.

The quality of farming grows logistically with a growth rate equal to the amount of farming at the site. I also assume farmed crops require maintenance, and if neglected the crops will eventually die. Thus, there is also a natural exponential decay term which is uninfluenced by the number or type of agents at the site. Therefore I have

$$q_{a,t+1} = q_{a,t} + \sum Y_a q_{a,t}(1 - \frac{q_{a,t}}{1}) - \delta q_{a,t}, \tag{6.6}$$

where δ is the farming decay rate. Hence, if there is no farming at the site the growth rate is zero, $\sum Y_a = 0$, and the site will eventually decay to $q_a = q_{a,min}$.

As in the previous model $q_a \in [q_{a,min}, 1]$ where $q_{a,min} > 0$. I will make the assumption that the minimum values for the foraging and farming qualities are the same ($q_{a,min} = q_{f,min}$).

6.1.5 The Maximum Number of Agents at a Site

In the previous model I had a parameter which defined the maximum number of agents that could survive at a site, n_{max}. This informed the fitness threshold for the death of an agent ($f_{min} = 1/n_{max}$), the carrying capacity of the system ($N_{max} = n_{max} s_x s_y$), and the initial population size ($N_{init} = \rho_{init} N_{max}$).

In this model n_{max} is the maximum number of foragers which can be supported at a site. ϕ more farmers can be supported than foragers, so the maximum number of farmers which can be supported at a site is

$$n_{a,max} = n_{max}\phi. \tag{6.7}$$

Since farming can support more agents than foragers, the maximum number of any agents that can survive at a site is also $n_{max}\phi$. Hence the carrying capacity of the whole region is $N_{max} = s_x s_y n_{max}\phi$, and the initial population size is $\rho_{init} s_x s_y n_{max}$.

In a foraging only region with n foragers ($\sum e = n$), the maximum number of foragers can occur when q_f is at its maximum and fitness is at its lowest, thus from Equation 6.2 the minimum fitness for this scenario will be

$$f_{min} = Y_f = 1/n_{max}. \tag{6.8}$$

For a farming only region with n farmers ($\sum(1 - e) = n$) the maximum number of farmers (where by definition $n \geq \phi$) will be when q_a is at its maximum and fitness is at its lowest. From Equation 6.3 the minimum fitness for this scenario will be

$$f_{min} = Y_a = \phi/n_{a,max}. \tag{6.9}$$

Substituting Equation 6.7 into Equation 6.9 I find

$$f_{min} = \phi/n_{max}\phi, \tag{6.10}$$

and thus in either case I have

$$f_{min} = \frac{1}{n_{max}}. \tag{6.11}$$

6.1.6 Initialisation

In the analysis of the Forager Model in Chapter 5, I considered the circumstances leading to the evolution of both high and low mobility in foragers. Thus, I began simulations with a random mobility strategy between 0.01 and 0.99. In this model however, I am specifically looking for the circumstances and pathways which lead to the evolution of farming from foraging, i.e. the transition to agriculture. Thus, I start all simulations with mobility and effort strategies of 0.99 – reflecting the Pleistocene state of mobile foragers. To introduce some variability there is one seed agent in the initial population which has an effort and mobility strategy of 0.8, this means that farming and reduced mobility have a chance to develop. Thus the initial mean strategies are high – which is especially the case when the initial density is high.

With these exceptions, the initial conditions are the same as for the Forager Model, i.e. initial agents occupy randomly chosen sites and have a fitness randomly selected between f_{min} to 1. The sites in the region have randomly chosen initial foraging qualities between $q_{f,min}$ and 1, and initial farming qualities between $q_{a,min}$ and 1. As before, the initial number of agents is $\rho_{init} n_{max} s_x s_y$, where ρ_{init} is the initial population density.

Thus ρ_{init} is a proportion of the maximum possible foragers, rather than maximum possible farmers.

6.1.7 Running the Model

Using the model described in this section I perform 5 experiments, these are summarised in Table 6.1. I perform some preliminary checks on the model to justify keeping the number of sites at 100, and the number of iterations at 1000. I describe and discuss these tests in Appendix K, and details of the coding of this model are given in Appendix C.

From some additional testing of the model I observed that for the evolution of farming to occur the farming decay rate, δ, needs to be small. Thus, I will only use low values for δ to make sure I have enough simulations to understand how farming can evolve.

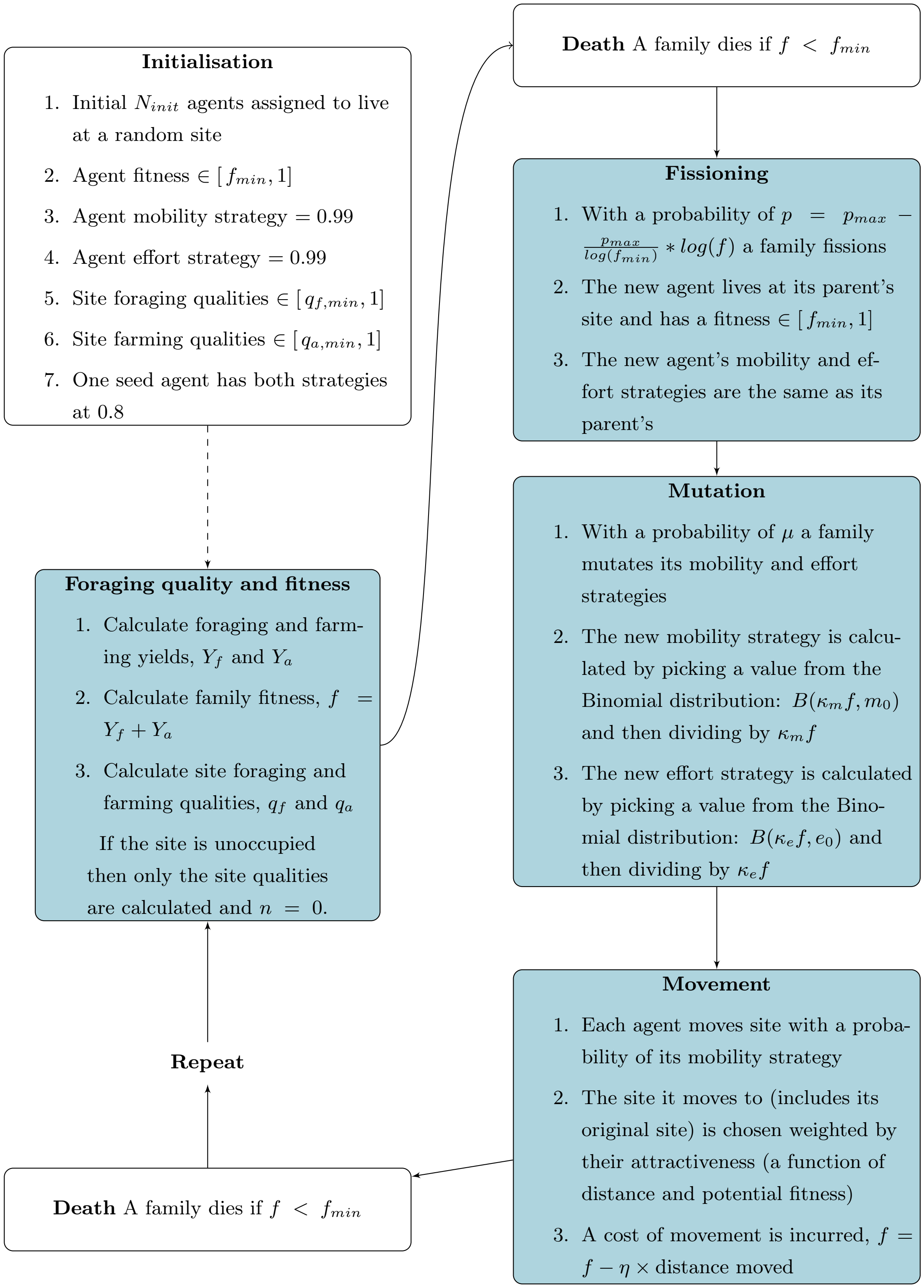
As in the Forager Model, I only analyse the simulations in which ≥ 15 agents were alive in the final iteration.

Table 6.1: A brief description of experiments using the subsistence strategy model. The table numbers refer to tables in Appendix M where all the details can be found.

Experiment number	Description	Table
1	Varying all 12 parameters	M4
2	Varying 4 parameters	M5
3	Looking at temporal variability	M6
4	Looking at spatial variability	M7
5	Simulations over time	M8

Table 6.2: Constants, variables and parameters in the model. Default values and whether they are found from data (D), predicted from the Forager Model (P), or assumed (A), are also given. Details about the data used are given in Table 2.4.

Constants		Range	Default value
s_x	Number of sites in x axis	-	-
s_y	Number of sites in y axis	-	-
d_{max}	Maximum distance of the region	Distance between bottom left and top right site	-
$q_{f,min}$	Minimum foraging quality		0.1 (P)
$q_{a,min}$	Minimum farming quality	$= q_{f,min}$	-
$n_{a,max}$	Maximum number of farmers which can be supported at a site	ϕn_{max}	-
N_{max}	Maximum number of families possible in the region	$n_{max}\phi s_x s_y$	-
N_{init}	Total number of agents initially	$\rho_{init} n_{max} s_x s_y$	-
f_{min}	Death fitness	$1/n_{max}$	-
Variables		**Range**	**Default value**
q_f	Site foraging quality	$[q_{f,min}, 1]$	-
q_a	Site farming quality	$[q_{a,min}, 1]$	-
m	Agent mobility strategy	$[0.01, 0.99]$	-
e	Agent effort strategy	$[0.01, 0.99]$	-
f	Agent fitness	$[f_{min}, 1]$	-
p	Probability of fission	$[0, p_{max}]$	-
$d_{a,b}$	Distance between site a and b	$[0, d_{max}]$	-
f^*	Potential fitness at a site	$(0, 1]$	-
A	Attractiveness of a site	$[0, 1]$	-
n	Number of agents at a site	$[0, N_{max}]$	-
Parameters		**Range**	**Default value**
r	Foraging quality growth rate	$[0, 1]$	-
λ	Foraging quality depletion scalar	$[0, 1]$	-
ϕ	How many times more farmers can be supported than foragers	≥ 1	5 (D)
β	Farming interference parameter	$[0, 1]$	-
δ	Farming decay rate	$[0, 1]$	-
κ_m	Mobility strategy conservatism	-	100 (P)
κ_e	Effort strategy conservatism	-	$= \kappa_m$ (A)
p_{max}	Maximum probability of fission	$[0, 1]$	0.14 (D)
η	Fitness cost of movement per site	$[0, 1]$	0.05 (P)
n_{max}	Maximum number of foragers which can be supported at a site	≥ 1	6 (D)
μ	Probability of mutation	$[0, 1]$	0.04 (A)
ρ_{init}	Initial population density	$(0, 1]$	0.1 (P)



Initialisation

1. Initial N_{init} agents assigned to live at a random site
2. Agent fitness $\in [f_{min}, 1]$
3. Agent mobility strategy $= 0.99$
4. Agent effort strategy $= 0.99$
5. Site foraging qualities $\in [q_{f,min}, 1]$
6. Site farming qualities $\in [q_{a,min}, 1]$
7. One seed agent has both strategies at 0.8

Foraging quality and fitness

1. Calculate foraging and farming yields, Y_f and Y_a
2. Calculate family fitness, $f = Y_f + Y_a$
3. Calculate site foraging and farming qualities, q_f and q_a

If the site is unoccupied then only the site qualities are calculated and $n = 0$.

Death A family dies if $f < f_{min}$

Fissioning

1. With a probability of $p = p_{max} - \frac{p_{max}}{log(f_{min})} * log(f)$ a family fissions
2. The new agent lives at its parent's site and has a fitness $\in [f_{min}, 1]$
3. The new agent's mobility and effort strategies are the same as its parent's

Mutation

1. With a probability of μ a family mutates its mobility and effort strategies
2. The new mobility strategy is calculated by picking a value from the Binomial distribution: $B(\kappa_m f, m_0)$ and then dividing by $\kappa_m f$
3. The new effort strategy is calculated by picking a value from the Binomial distribution: $B(\kappa_e f, e_0)$ and then dividing by $\kappa_e f$

Movement

1. Each agent moves site with a probability of its mobility strategy
2. The site it moves to (includes its original site) is chosen weighted by their attractiveness (a function of distance and potential fitness)
3. A cost of movement is incurred, $f = f - \eta \times$ distance moved

Death A family dies if $f < f_{min}$

Repeat

6.2 Parameters Sensitivity and Simulation Outcomes

To separate simulations by type of outcomes I use both the Outcome Clustering method (as described in Section 2.4.4) and the FIO method. In the Forager Model I had four model outcomes to predict simulation cluster (final number of agents, final mean mobility strategy, final mean fitness and final mean foraging quality). In this analysis I have two additional outcomes – the final mean effort strategy and the final mean farming quality. I use the FIO method to specifically find the circumstances under which certain strategies develop (including sedentary farming).

In this section I will present the methods and results of the experiment in which I vary all 12 parameters, and the experiment where I fix certain parameter values and only vary four parameters.

6.2.1 The Effect of All 12 Parameters – Experiment 1

I ran the model 10,000 times whilst varying all 12 of the parameters (see Table M4 in the Appendix for the full details of this run). Out of these simulations 6390 had ≥ 15 agents alive in the final iteration.

The frequencies for each of the outcomes are shown in Figure 6.2, and the relationship between final mean effort and mobility strategies are shown in Figure 6.3. I give the correlation coefficients between all parameters and outcomes in Table 6.3. I find that most simulations either have high effort and mobility strategies, or low effort and mobility strategies, and those that fall outside of these extremes lie somewhere in between (the correlation coefficient is $\rho = 0.864$). Apart from the null strategy, most outcomes are highly correlated.

There are several strong correlations between the parameters and outcomes; for example the maximum number of agents (n_{max}) and fitness (f), $\rho = -0.665$; and the farming decay rate (δ) and the farming quality (q_a), $\rho = -0.525$. These could be explained by direct effects, such as large populations meaning the site qualities have to be shared between more people, and thus reducing fitness. Of the four parameters which directly effect the foraging and farming qualities (r, λ, β and δ), it is only δ which has any strong linear correlations with outcomes.

The results presented in the rest of this chapter often use colour coding to represent both the final mean mobility and final mean effort strategies of the simulations. This colour coding can be seen in Figure 6.4. Unless otherwise stated, please refer to this figure for colour coding.

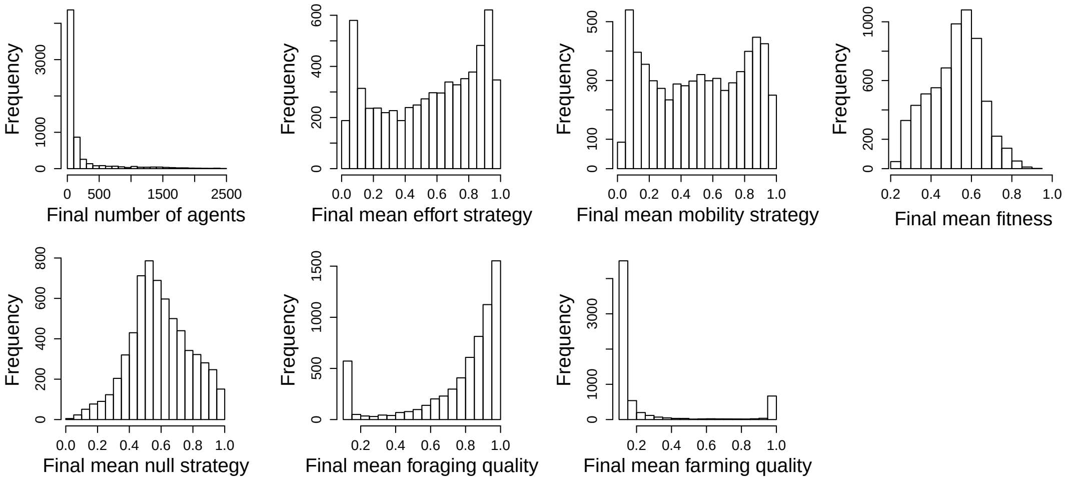


Figure 6.2: Histograms of the outcomes of simulations with ≥ 15 agents alive in the final iteration, when varying all the parameters.

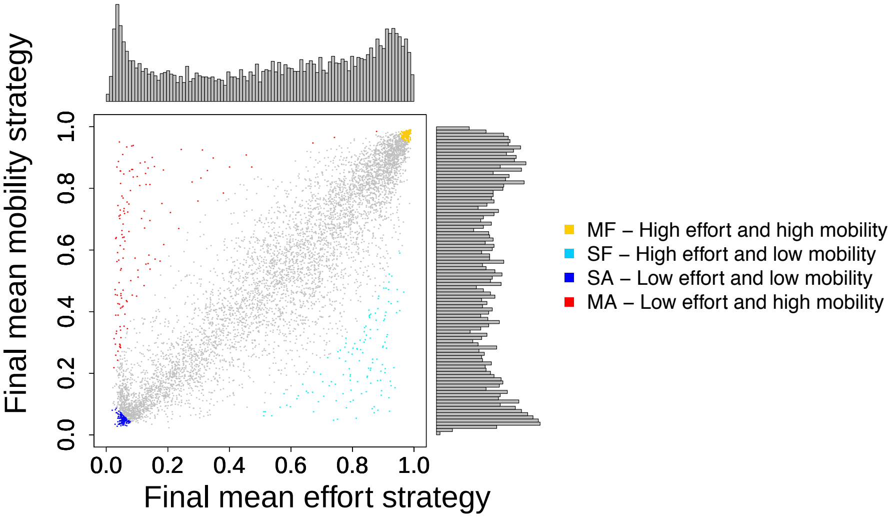


Figure 6.3: Final mean effort strategy by final mean mobility strategy for all simulations with ≥ 15 agents alive in the final iteration, when varying all the parameters. 2% (128) of the simulations from each of the extreme strategies are coloured according to the key.

Table 6.3: Pearson product-moment correlation coefficients for every combination of parameters and outcomes in the 6390 simulations with ≥ 15 agents alive in the final iteration, when all parameters are varied. *** p-value < 0.001, ** p-value < 0.01, * p-value < 0.05.

	r	λ	ϕ	β	δ	κ_m	κ_e	p_{max}	η	n_{max}	μ	ρ_{init}
λ	0.009											
ϕ	-0.004	0.002										
β	-0.003	-0.01	0.005									
δ	0.029*	-0.001	-0.037**	-0.022								
κ_m	0.004	0.015	-0.023	-0.001	-0.014							
κ_e	0.022	0.012	0.002	0.006	0.007	-0.005						
p_{max}	0.004	0.01	-0.001	-0.008	-0.013	0.022	0.014					
η	-0.001	0.01	0.041**	-0.019	-0.001	-0.022	-0.001	0.016				
n_{max}	-0.051***	0.102***	-0.025*	-0.025*	0.032**	-0.01	0.016	-0.099***	0.223***			
μ	-0.012	0	0.017	-0.014	-0.028*	0.012	-0.019	0.016	0.025*	-0.008		
ρ_{init}	-0.049***	0.051***	-0.002	0.018	0.047***	0	-0.013	-0.075***	0.145***	-0.078***	0.003	
Final number of agents	0.083***	-0.089***	0.234***	-0.042***	-0.369***	-0.006	-0.009	0.104***	-0.204***	0.226***	0.088***	-0.004
Final mean effort strategy	0.009	-0.034**	-0.217***	0.08***	0.477***	0.017	0.075***	-0.08***	-0.264***	-0.302***	-0.341***	-0.062***
Final mean mobility strategy	-0.045***	0.075***	-0.207***	0.076***	0.359***	0.079***	0.024	0.032**	-0.318***	-0.38***	-0.368***	-0.06***
Final mean fitness	-0.036**	0.015	-0.178***	0.083***	0.262***	0.026*	-0.003	-0.148***	-0.12***	-0.665***	-0.138***	0.117***
Final mean null strategy	0.008	0.013	-0.018	0.014	0.027*	0.13***	-0.016	-0.005	-0.021	-0.053***	-0.475***	0.014
Final mean foraging quality	0.068***	-0.042***	-0.062***	0.007	0.396***	-0.01	0.023	-0.174***	0.453***	-0.18***	-0.07***	0.041**
Final mean farming quality	0.079***	-0.086***	0.058***	-0.044***	-0.525***	0.003	-0.033**	0.108***	-0.192***	0.137***	0.114***	-0.023

	Final number of agents	Final mean effort strategy	Final mean mobility strategy	Final mean fitness	Final mean null strategy	Final mean foraging quality
Final mean effort strategy	-0.551***					
Final mean mobility strategy	-0.483***	0.864***				
Final mean fitness	-0.573***	0.678***	0.704***			
Final mean null strategy	-0.112***	0.273***	0.313***	0.175***		
Final mean foraging quality	-0.762***	0.482***	0.316***	0.475***	0.087***	
Final mean farming quality	0.823***	-0.664***	-0.513***	-0.495***	-0.117***	-0.864***

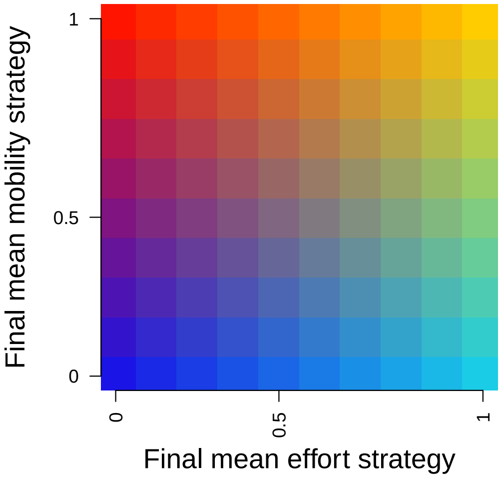


Figure 6.4: Colour coding used to represent final mean strategies.

Extreme Strategies

I used the Outcome Clustering method described in Section 2.4.4 to find clusters of simulations using the six outcomes (final number of agents, mean effort and mobility strategies, mean fitness, foraging quality and farming quality). This analysis revealed a cluster with high numbers of agents, low final mean effort and mobility strategies, low final mean fitness, low final mean foraging quality, and high final mean farming qualities. However, the algorithm did not highlight a cluster with the opposite qualities, and thus I could not make predictions about how mobile foraging could remain the dominant strategy. More results from this analysis are discussed in Appendix L.

Alternatively to the clustering approach, I used the FIO method to separate simulation types. Although my key question concerns the evolution of sedentary farming, I look at four types of idealised outcomes in this analysis:

1. MF simulations – high mobility and high effort strategies (mobile foragers)
2. MA simulations – high mobility and low effort strategies (mobile agriculturalists[1])
3. SF simulations – low mobility and high effort strategies (sedentary foragers)
4. SA simulations – low mobility and low effort strategies (sedentary agriculturalists)

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[1] I interchange the word ‘farmer’ with ‘agriculturalist’ for the purpose of making the acronym distinct

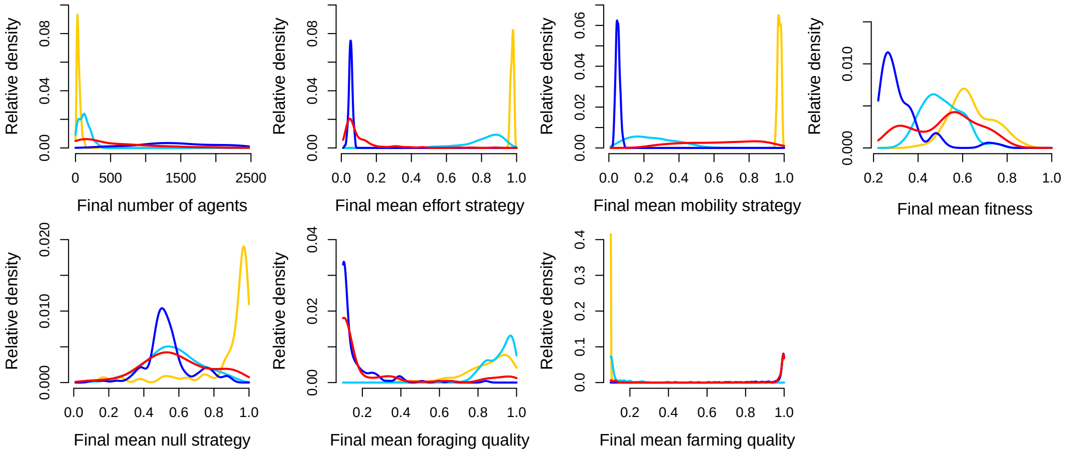
I took the most extreme ('top') 2% (128) of simulations from each of these four simulation types and compared their outcome and parameter values. When I refer to the 'SA set' I specifically mean the 2% of simulations with the lowest of these values (measured by Euclidean distance from strategies of 0.99).

I show the relative frequencies for the outcomes and parameters of these sets in Figure 6.5. A clear distinction in the outcomes of these sets is that when there is a high mean effort strategy (mostly foraging) the final mean foraging quality is high and the final mean farming quality is low, and when there is a low mean effort strategy (mostly farming) the final mean foraging quality is low and the final mean farming quality is high.

Parameter distributions can be different for the simulation sets – this is shown in Figure 6.5b. Some parameters strongly influence the outcomes (e.g. the foraging depletion rate, λ, is very low in SF simulations; the farming decay rate, δ, is very low in low effort simulations; and the mutation rate, μ, is very low in MF simulations), and others do not make much difference (e.g. the conservatism parameters, κ_m and κ_e; and the farming interference parameter β).

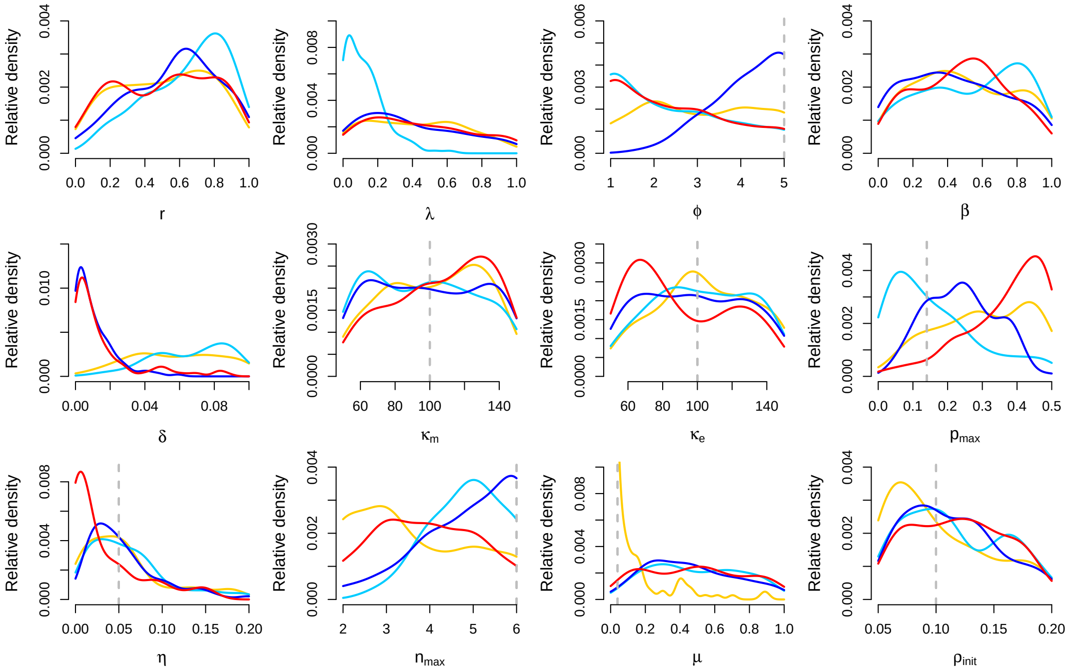
The fact that the mutation rate, μ, is low in MF simulations suggests that perhaps one of the main reasons these are MF simulations is that they were not able to mutate much from the initial state (where every agent is a mobile forager). Thus, it is worth remembering these MF simulations may have not evolved to optimal strategies, but rather not changed at all. I fix μ in the next section and thus these effects are eradicated.

I examined the relationships between each pair of outcomes for all of the simulations, this can be seen in Figure 6.6. I find that the largest numbers of agents co-occur with low strategies, fitness and foraging quality, but high farming quality. Foragers tend to have higher fitnesses than farmers, and highly mobile agents tend to have higher fitnesses than sedentary agents. Also I find that farming and foraging quality are negatively correlated.



(a) Outcomes in different extremes.

🟨 MF – High effort and high mobility
🟦 SF – High effort and low mobility
🟦 SA – Low effort and low mobility
🟥 MA – Low effort and high mobility



(b) Parameters in different extremes. Grey dashed lines show default values.

Figure 6.5: The outcomes (a) and parameters (b) in the top 2% (128) of each of the extreme simulation types, using all the 6390 simulations with ≥ 15 agents alive in the final iteration when all parameters are varied. Grey dashed lines show default parameter values (if given).

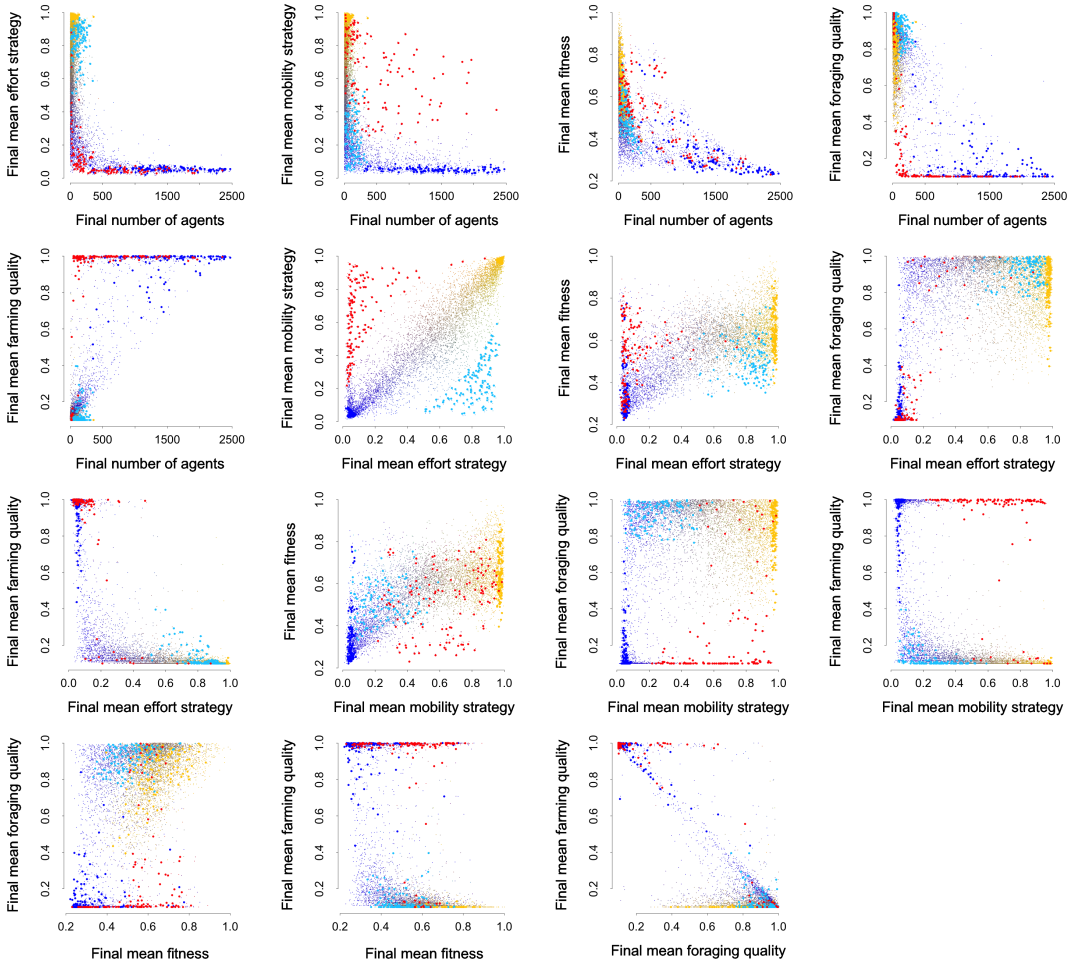


Figure 6.6: Outcome pairs in all simulations, using all the 6390 simulations with ≥ 15 agents alive in the final iteration when all parameters are varied. Points from the top 2% (128) of each of the extreme simulation types are slightly larger. Coloured by the final mean strategies for the simulation (see Figure 6.4).

6.2.2 Fixing Parameters – Experiment 2

I decided to normalise the effects from population size, mutation of strategies and movement costs, in order to see the influences of the environmental parameters more clearly. Thus in Experiment 2 I fixed the parameters, ϕ, κ_m, κ_e, p_{max}, η, n_{max}, μ, and ρ_{init} to their default values of 5, 100, 100, 0.14, 0.05, 6, 0.04 and 0.1 respectively. I varied r, λ, β and δ randomly in 100,000 simulations (Table M5 in the Appendix gives exact inputs for this experiment). Of these simulations 98,927 had ≥ 15 agents alive in the final iteration.

The outcome frequencies for these simulations are shown in Figure 6.7, and the relationship between the effort and mobility strategies are shown in Figure 6.8. The correlation coefficients between the parameters and outcomes in these simulations are given in Table 6.4.

I find that fixing the parameters to these values mean that more of the simulations have mean strategies in the extremes, i.e. there are less simulations with mid values for their final mean strategy values. I also find that the final mean strategies are less strongly linearly correlated. In particular I find many more simulations in the SF set, which may be explained by setting $p_{max} = 0.14$ or $n_{max} = 6$ (since I showed these values were common in SF simulations from Figure 6.5b). Again, I find that many of the outcomes are highly correlated.

Since the mutation rate is relatively low I find that the mean null strategy is often higher in this experiment compared to Experiment 1, where the mean null strategy was more frequently at a mid value. This result is reassuring as it means that when the effort or mobility strategies are low or at a mid value, it is a product of selection rather than drift. It could also explain the large number of simulations with mid strategy values in Experiment 1 – these may have occurred by drift.

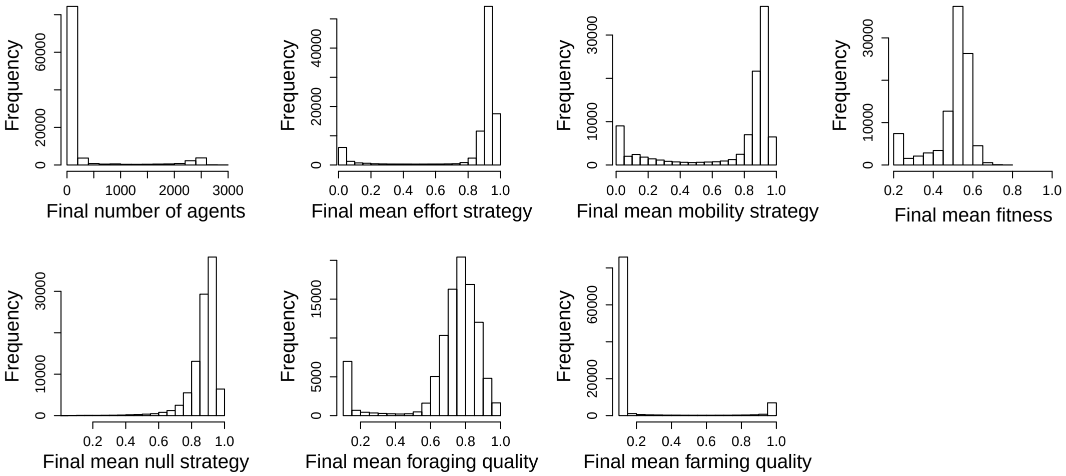


Figure 6.7: Output histograms of all simulations with ≥ 15 agents alive in the final iteration, when 4 parameters are varied.

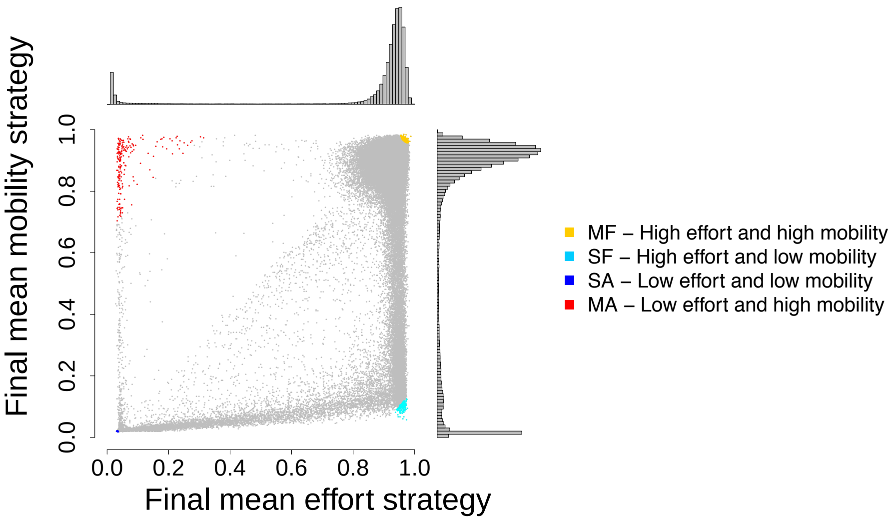


Figure 6.8: Final mean effort strategy by final mean mobility strategy for all simulations with ≥ 15 agents alive in the final iteration, when 4 parameters are varied. 0.2% (198) of the simulations from each of the extreme strategies are coloured according to the key.

Table 6.4: Pearson product-moment correlation coefficients for every combination of parameters and outcomes in the 98,927 simulations with ≥ 15 agents alive in the final iteration. When 4 parameters are varied. *** p-value < 0.001, ** p-value < 0.01, * p-value < 0.05.

	r	λ	β	δ	Final number of agents	Final mean effort strategy	Final mean mobility strategy	Final mean fitness	Final mean null strategy	Final mean foraging quality
λ	0.01***									
β	0.00	0.00								
δ	0.00	0.00	0							
Final number of agents	0.18***	-0.28***	-0.08***	-0.36***						
Final mean effort strategy	-0.13***	0.24***	0.08***	0.36***	-0.96***					
Final mean mobility strategy	-0.23***	0.54***	0.04***	0.19***	-0.75***	0.74***				
Final mean fitness	-0.17***	0.4***	0.06***	0.27***	-0.86***	0.85***	0.85***			
Final mean null strategy	-0.03***	0.10***	0.02***	0.08***	-0.26***	0.26***	0.25***	0.27***		
Final mean foraging quality	0.09***	0.02***	0.06***	0.38***	-0.86***	0.88***	0.50***	0.71***	0.22***	
Final mean farming quality	0.15***	-0.24***	-0.07***	-0.40***	0.97***	-0.97***	-0.72***	-0.83***	-0.25***	-0.90***

I looked at the relationships between pairs of simulation outcomes in Figure 6.9. Many of these relationships are generally the same as when I varied all 12 of the parameters, but also reveal intricacies unseen before. It can also be seen that when the effort strategy is high (i.e. only looking at the yellow to light blue points) the plots are comparable to Figure 5.16b from the Forager Model.

Generally these plots show a continuum of properties between SF and SA simulations (light blue to dark blue), and another continuum between MA to SA simulations (red to dark blue). The biggest difference between these two is that MA to SA simulations have higher numbers of agents. There is also quite a strong cluster of SF simulations (yellow).

In Figure 6.10 I plot the relationships between pairs of parameters and colour by the final mean strategy values. It can be seen that the relationship between r and λ is similar to as in the Forager Model (see Figure 5.18) – the least mobile simulations have the highest r and λ ratio (i.e. the growth rate is higher than the depletion rate). I also find that β makes little difference to the end strategies, and SA simulations have the lowest values of δ.

In Figure 6.11 I plotted the relationships between parameter values and the Euclidean distance between the beginning strategies (taken as 0.99 for both) and the final strategies. This plot further highlights the effect of high r and low λ causing the most changes in strategy value, and the biggest changes (SA simulations) have the lowest values for δ.

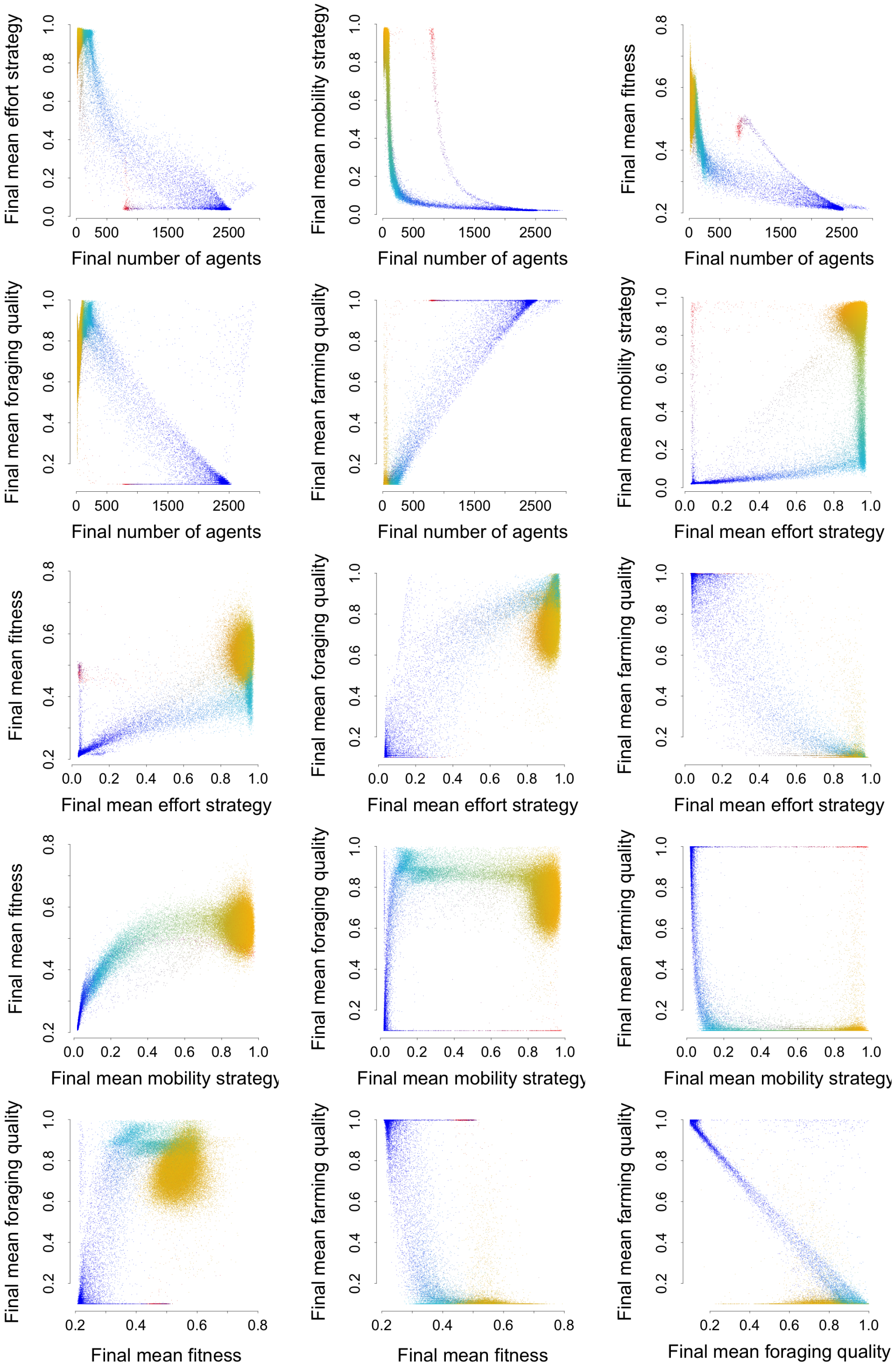


Figure 6.9: Pairwise relationships between all outcomes using all simulations with ≥ 15 agents alive in the final iteration, when 4 parameters are varied. Coloured by the final mean strategies for the simulation (see Figure 6.4).

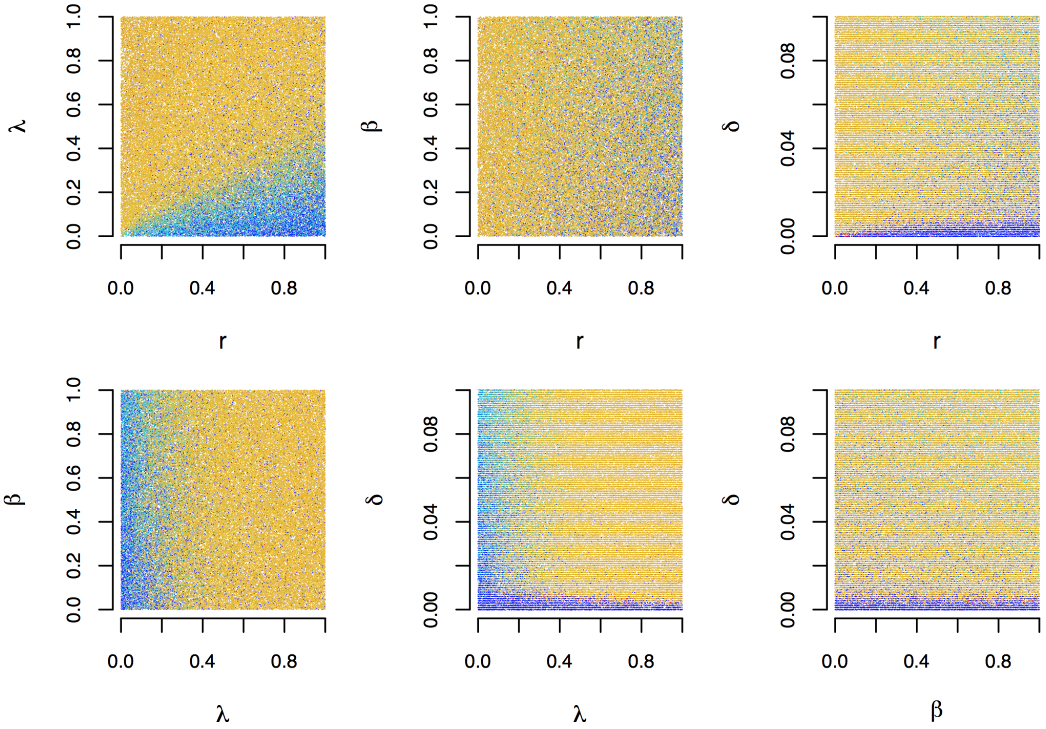


Figure 6.10: Pairwise relationships between all parameters using all simulations with ≥ 15 agents alive in the final iteration, when 4 parameters are varied. Coloured by the final mean strategies for the simulation (see Figure 6.4).

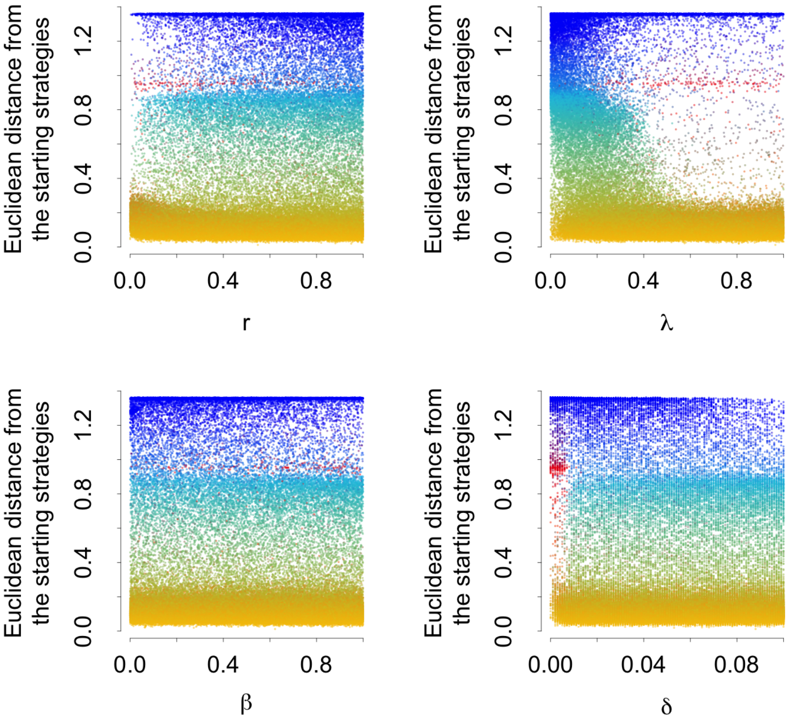


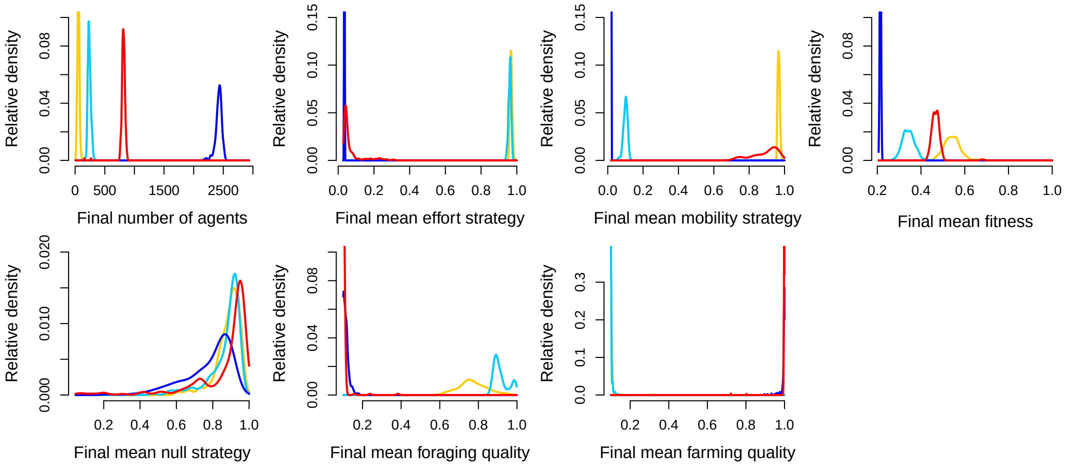
Figure 6.11: Relationships between parameters and the Euclidean distances from the starting effort and mobility strategies and the final mean values in all simulations with ≥ 15 agents alive in the final iteration. Coloured by the final mean strategies for the simulation (see Figure 6.4).

Extreme Strategies

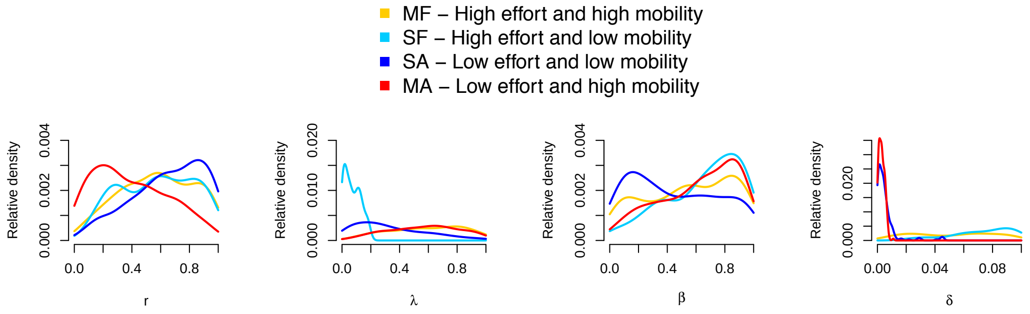
The clustering analysis for this experiment managed to pick out high and low effort strategies, but as in Experiment 1, was not so successful in picking out high and low mobility strategies. Because of this I will focus my discussion on the results from using the FIO approach, where my four idealised outcomes are the simulations with the most extreme strategies – highly mobile foragers, highly mobile farmers, highly sedentary foragers and highly sedentary farmers.

I look at the top 0.2% of simulations (198 simulations) from each of the four extreme strategies. Figures 6.12a and 6.12b show the relative densities of outcomes and parameter values respectively for each of these.

The lowest values for the farming decay rate, δ, are seen in the farming extremes – the MA and SA sets. And the lowest values for the foraging depletion rate, λ, are seen in the SF set. By looking at the pairwise relationships between parameters in these sets, in Figure 6.13, I can see that although the SA set has slightly higher values for r and slightly lower values for λ than in the MA set, the relationships are very similar. Thus, farming evolves in the best environments for farming and sedentism evolves in the best environments for foraging. I also find that low numbers of agents are found when there is more foraging, and high number are found when there is more farming. Additionally, when there is high mobility then these numbers are even lower.



(a) Relative densities of outcomes for the different extremes.



(b) Relative densities of parameters for the different extremes.

Figure 6.12: The outcomes (a) and parameters (b) in the top 0.2% (198) of each of the extreme simulation types, using all the 98,927 simulations with ≥ 15 agents alive in the final iteration when four parameters are varied.

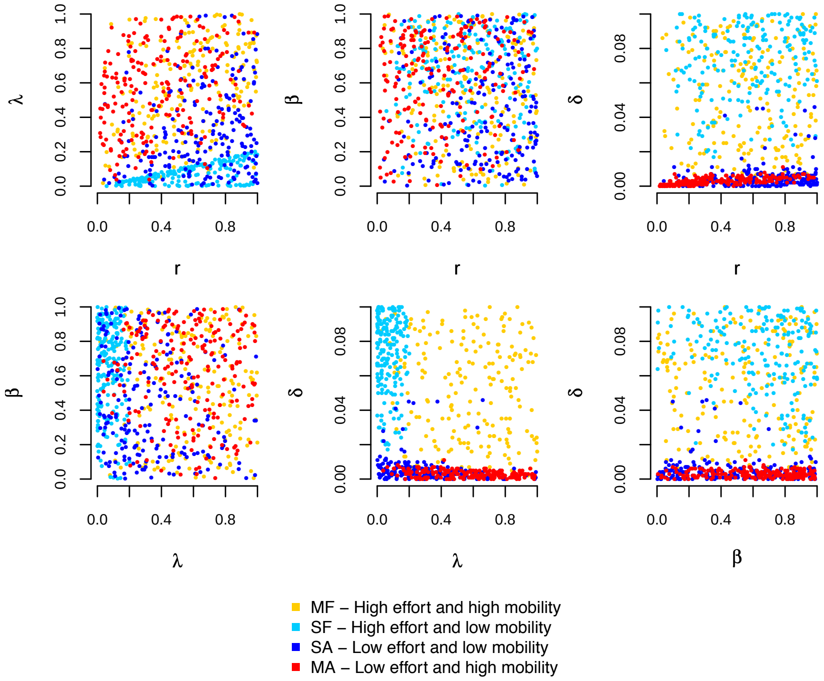


Figure 6.13: Parameter pairs in the top 0.2% (198) of each of the extreme simulation types, using all the 98,927 simulations with ≥ 15 agents alive in the final iteration when four parameters are varied.

6.3 Temporal and Spatial Variability

In this section I investigate the effects from temporal and spatial environmental variability on the outcomes of my model.

6.3.1 Temporal Variability – Experiment 3

I ran the model 10,000 times over 1000 iterations, this left 9899 simulations with ≥ 15 agents alive in the final iteration. Other details of this run of the model are given in Table M6. In this model I implemented temporal variation slightly differently to in the Forager Model. As before I picked new parameter values randomly in $[\text{previous value} - WD, \text{previous value} + WD]$, where WD is the random walk distance. I varied all the environmental conditions, r, λ, β and δ like this. Rather than allowing there to be a run in time where there was no variation in the environmental conditions, I set it so variability began in the first iteration. Also, rather than the binary 'variation' or 'no variation' and setting the walk distance to 0.1, I varied the walk distance every simulation between 0 and 1. In this way I was able to investigate the different extremes of variation – since if $WD = 0$ there is no variation, and if $WD = 1$ there is a lot of variation from iteration to iteration. The results from this can be seen in Figure 6.14.

I found that little temporal variation means that there are more SA and SF simulations. This is strongest for the SF simulations, where there are none of these simulations when there is a high amount of temporal variation. In this experiment there were not any MA simulations, so perhaps temporal variation also negatively impacts the emergence of these too. Thus, temporal variation disrupts the evolution of sedentary foraging, and to a lesser extent, sedentary farming.

6.3.2 Spatial Variability – Experiment 4

Including spatial variability in this model is slightly different than in the Forager Model since in the Forager-Farmer Model there are more environmental variables to vary. In the previous sections I found that β had limited effect on the outcomes, so I only considered r, λ and δ when looking at spatial variability. To look at each pair of these required three runs of the model – varying r and λ, varying r and δ, and varying λ and δ – these are the 'structured spatial variability' simulations. I varied β between 0 and 1 every time. I also ran the model with 'non-structured spatial variability' (each site has randomly chosen values for r, λ and δ) and 'no variability' (the usual type of run where every simulation has the same randomly chosen parameter values for every site), these

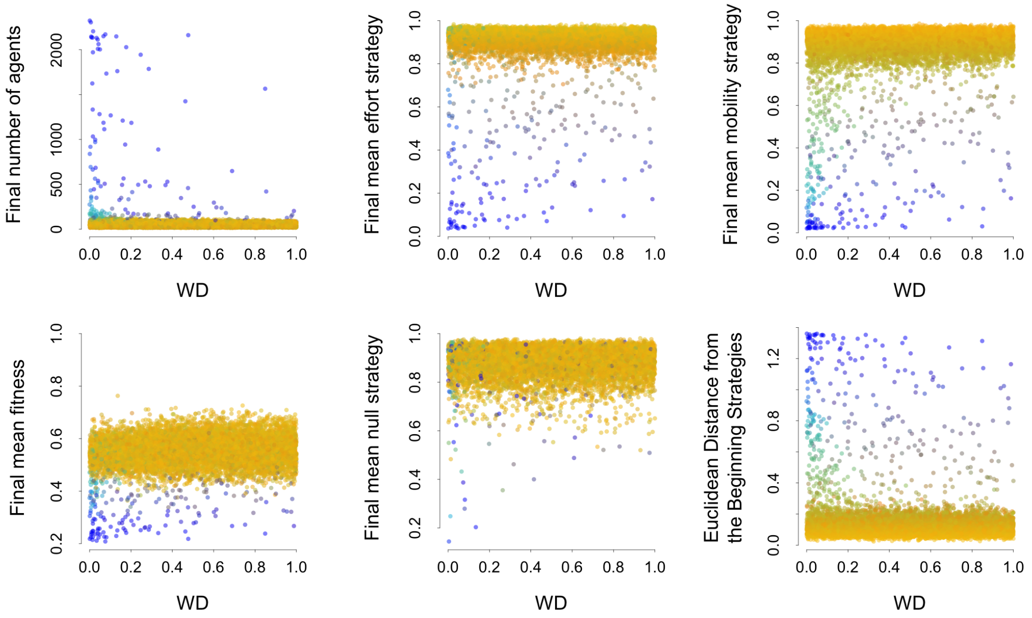


Figure 6.14: Simulation outcomes when varying the walk distance (WD) in the random walk. Using all simulations with $\geq$ 15 agents alive in the final iteration, when 4 parameters are varied. Coloured by the final mean strategies for the simulation (see Figure 6.4).

are illustrated in Figure 6.15 and all details of the experiment are given in Table M7. Each of these five model conditions were run 10,000 times over 1000 iterations.

I found that no spatial variability led to the highest percentage (10.3%) of low strategy simulations (which I define here as having both final mean strategies < 0.5), r and λ spatially structured variability had 6.5% low strategy simulations, r and δ spatially structured had 4.5%, non-structured simulations had 2.1%, and lastly λ and δ spatially structured had 1.7%.

In Figure 6.16 I plotted the final mean strategies for each of these five simulation types. I found that non-structured spatial variability gives simulations in a continuum between being a mobile forager and a sedentary farmer, and there are little to no MA or SF simulations. SF simulations do not occur very often when there is structured spatial variability in λ; and SA and MA simulations do not occur as often when there is variability in δ.

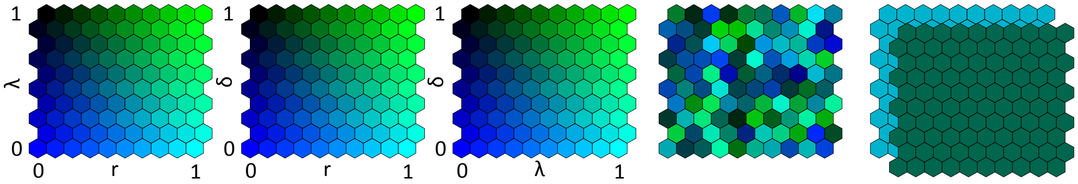


Figure 6.15: Values for r, λ and δ at each site in the structured (first, second and third grids), non-structured (fourth grid) spatial variability, and no variability (last grid, where each simulation will have a different value) runs of the model. For the non-structured and no variability runs of the model these values are picked randomly for each each simulation.

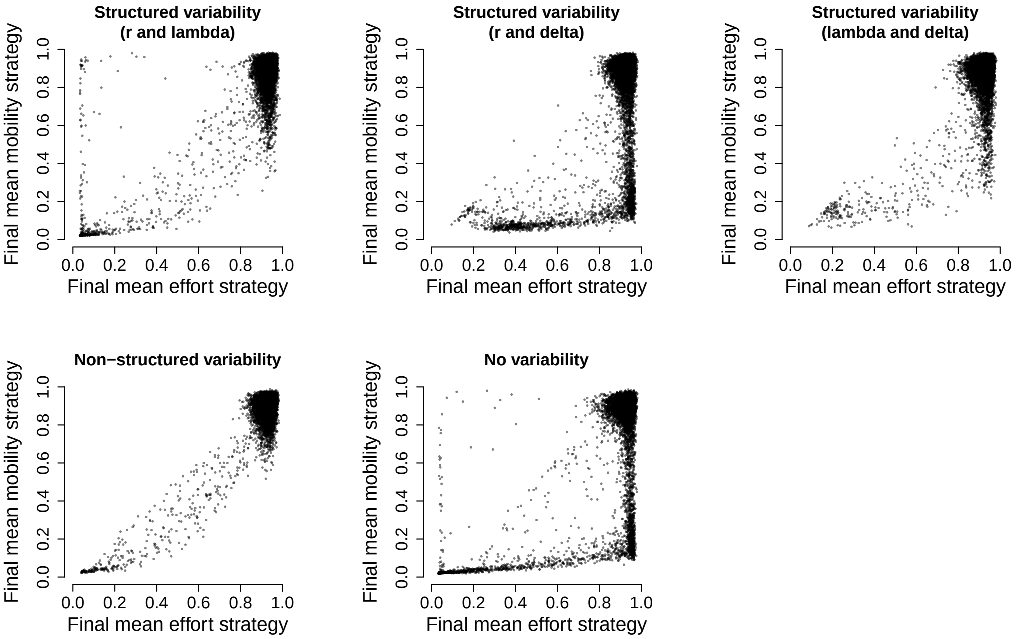


Figure 6.16: The final mean effort and mobility strategies in each of the three structured spatial variability (where r and λ change, where r and δ change, and where λ and δ change), the non-structured spatial variability and the non-variability runs of the model. Each point represents a simulation.

6.4 Model Events Over Time

So far I have investigated the parameter values in four types of simulation; MF, SF, MA and SA simulations. In this section I will investigate the processes which lead to these simulation outcomes.

6.4.1 Dynamics Over Time – Experiment 5

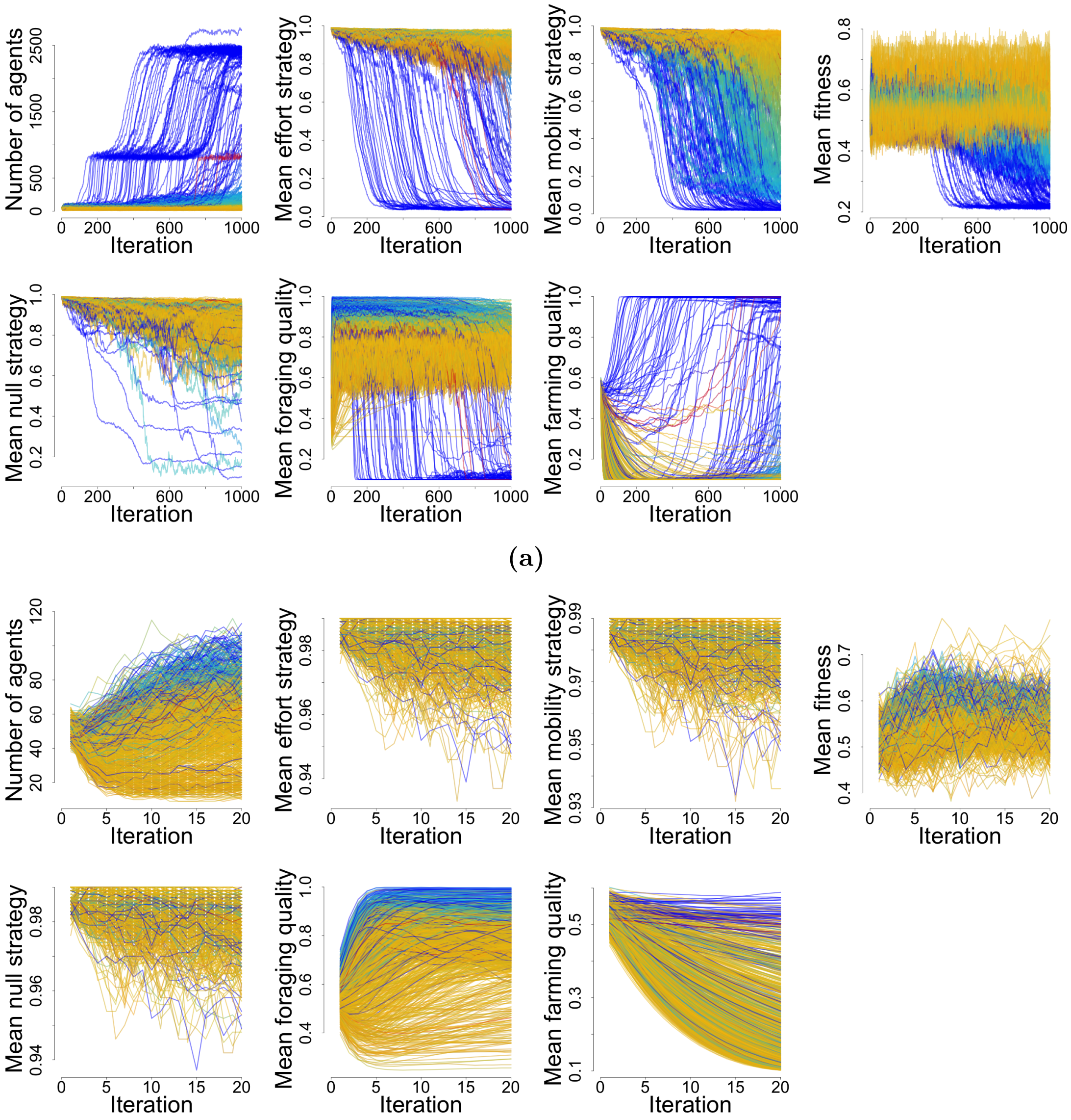
I ran the model 1000 times over 1000 iterations and looked at how outcomes change over time (rather than focusing on the final iteration). Details of this experiment are given in Table M8. Figure 6.17 shows the mean outcomes of 1000 simulations over time for all 1000 iterations and for just the first 20 iterations. There is a short settling in period where the number of agents decreases slightly, the fitness increases and site qualities also change. After this there are big changes in the simulations that become sedentary farmers – these increase in numbers, and decrease in effort and mobility strategies, fitness, and foraging quality. There is then a second increase in the number of agents. The farming quality for these decreases and then increases.

SA simulations have two levels in their number of agents, and the SF simulations never have as high population numbers as the first plateau of the SA simulations. The MF to SF simulations (yellow to light blue) follow similar patterns as those of the Forager Model (Figure 5.24). I estimate the SF simulations get to as many as around 300 agents, and SA simulations have plateaus of around 800 agents and 2500 agents.

I looked at how the mean mobility and effort strategies changed over time for all of the simulations. This is shown in Figure 6.18a where I plot the mean strategies every 100 iterations, and in Figure 6.18b where the mean strategies for every iteration are plotted. By finding the mean ratio of the strategies over all iterations for each simulation, I can find how many usually have higher effort strategies than mobilities and vice versa. Figure 6.19a shows the average ratio over time for each simulation. There were a majority (722 to 278) of simulations which had a mean ratio of less than 1, which suggests for most of the time their effort strategy was higher than their mobility strategy. However, when I only looked at low strategy simulations (defined here by both the final mobility strategy and the final effort strategy being < 0.5) the number with a mean ratio of less than 1 was 50 whilst the number greater than 1 was 45. Figure 6.19b shows how it is only for the MF simulations for which the mean ratio is around 1. Hence, when SA simulations evolve they do so according to one of two pathways – becoming sedentary first and then farmers, or farming first then sedentary. From Figure 6.18a I can see that the evolution of SA simulations via farming first generally happens before the evolution of SA simulations via becoming sedentary first.

I also looked at the parameters which were in each of the simulations in Figures 6.19c and 6.20. From these the distinctions between the SA simulations which became sedentary first and the SA simulations which became farmers first can be seen. The main difference is that when farming occurs first it is when the value for δ is particularly low. Also when SA simulations evolve by becoming sedentary first they tend to have lower λ values and higher r values than those that remain sedentary foragers.

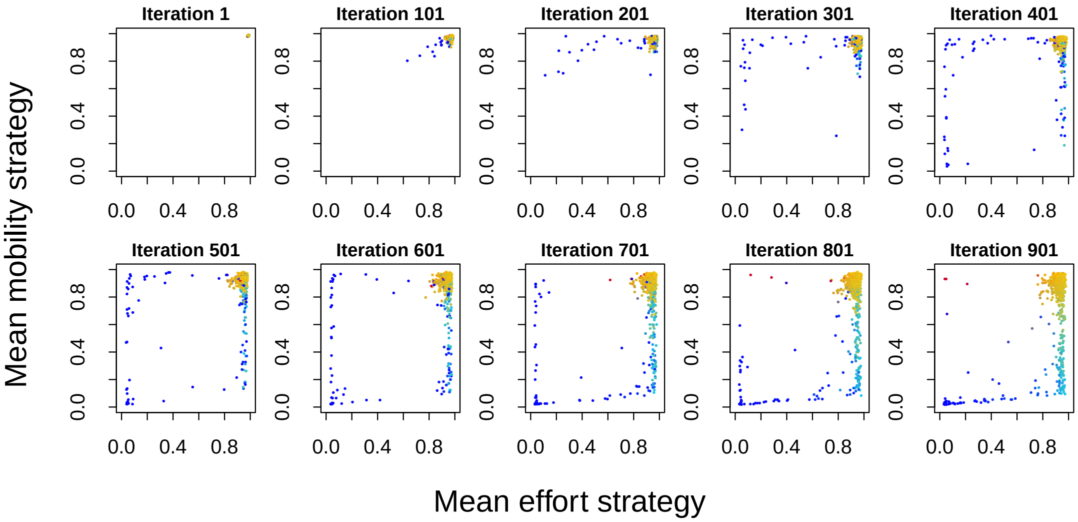
In Figure 6.21 I looked at the number of agents over time in both the SA simulations, where the mean mobility to effort ratio is less than 1, and when it is greater than 1. This plot shows that when farming occurs before sedentism (when the ratio is greater than 1) there are two steps to the population size increase – once for when farming occurs, and once for when sedentism occurs. When sedentism occurs before farming there is only one population size increase.



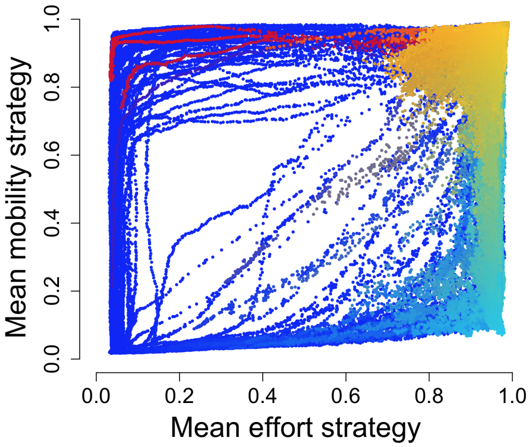
(a)

(b)

Figure 6.17: Outcomes at all 1000 iterations (a), and at the first 20 iterations (b), for each of the 1000 simulations. Coloured by the final mean strategies for the simulation (see Figure 6.4).

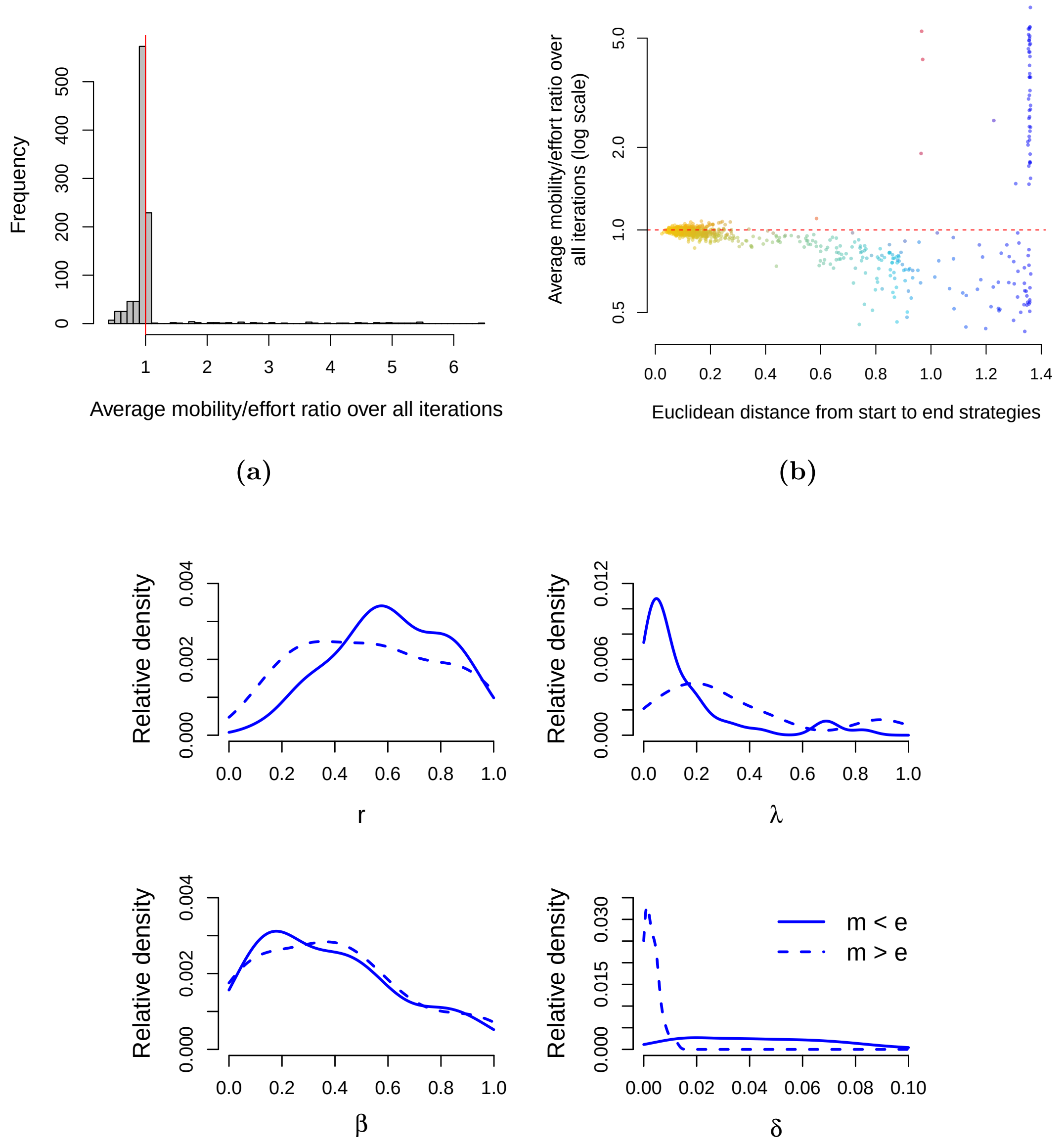


(a)



(b)

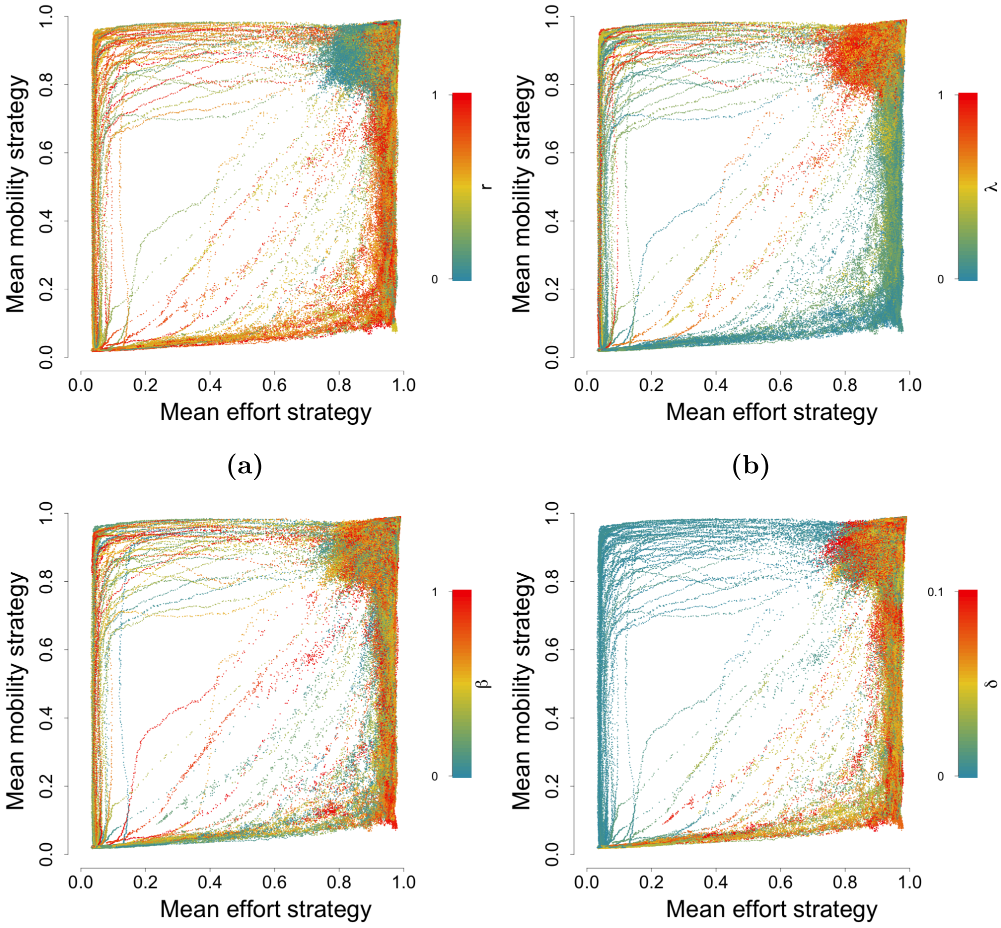
Figure 6.18: Pathways of evolution. Mean strategies for each simulation at various iterations (a) and all the iterations (b). Points are coloured by the final mean strategies for the simulation (see Figure 6.4).



(a) **(b)**

(c)

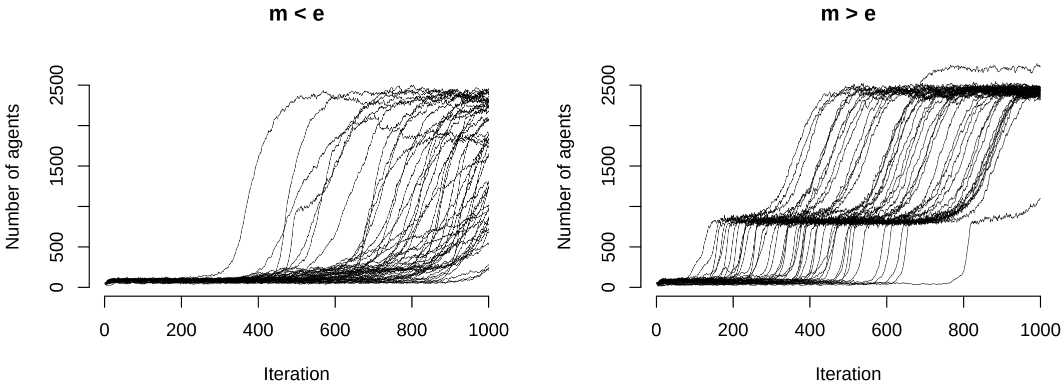
Figure 6.19: The average mobility to effort strategy ratios over all iterations, for each of the 1000 simulations. (a) A histogram of this ratio. (b) The relationship between the Euclidean distance between start and end strategies and the ratio, coloured by the final mean strategies for the simulation (see Figure 6.4). 722 simulations have an average ratio of less than 1, and 278 have a ratio greater than 1. (c) The parameter densities in the SA simulations (strategies < 0.5, 95 simulations) where the average mobility to effort strategy ratio is < 1 (50 simulations) and > 1 (dashed, 45 simulations).



(a) (b)

(c) (d)

Figure 6.20: The trajectories of strategy values for each simulation coloured by the parameter values.



(a)

Figure 6.21: The number of agents over time in the simulations with final mean strategies are < 0.5, for both those when the average mobility to effort strategy ratio is less than 1 (left, 50 simulations) and greater than 1 (right, 45 simulations)

Table 6.5: The percentage of times different simulation outcome orders occurred. Given for all 1000 simulations, only the 95 SA simulations (defined as when the final mean mobility and effort are both ≤ 0.5), and only the 110 SF simulations (defined as when the final mean mobility is ≤ 0.5 and final mean effort is > 0.5).

Order	Percentage of all simulations	Percentage of SA simulations	Percentage of SF simulations
$\bar{e}$ then N	89%	92%	85%
$\bar{m}$ then N	92%	93%	91%
$\bar{f}$ then N	45%	57%	40%
$\bar{f}$ and N	25%	29%	26%
$\bar{e}$ and $\bar{m}$	80%	78%	70%
$\bar{e}$ then $\bar{f}$	53%	46%	62%
$\bar{e}$ and $\bar{f}$	38%	49%	32%

6.4.2 Ordering Model Events

I applied the same algorithm as I did for the Forager Model (explained in Section 2.4.2) to predict which order the model events occurred in. I found that in general the mean strategies change at the same time, then the mean fitness changes and then (or at the same time) the number of agents changes. The percentage of simulations found in various orders are shown in Table 6.5 and Figure 6.22 gives a pair-wise comparison of when outcome changes occurred.

The fact that this algorithm has picked out the effort and mobility strategy as changing at the same time may actually be an artefact of the low resolution (if anything changes within 100 iterations of each other this algorithm can group them as occurring at the same time). Thus the main message from this analysis is that despite the low resolution, the number of agents and the fitness change after the mobility and effort strategies do.

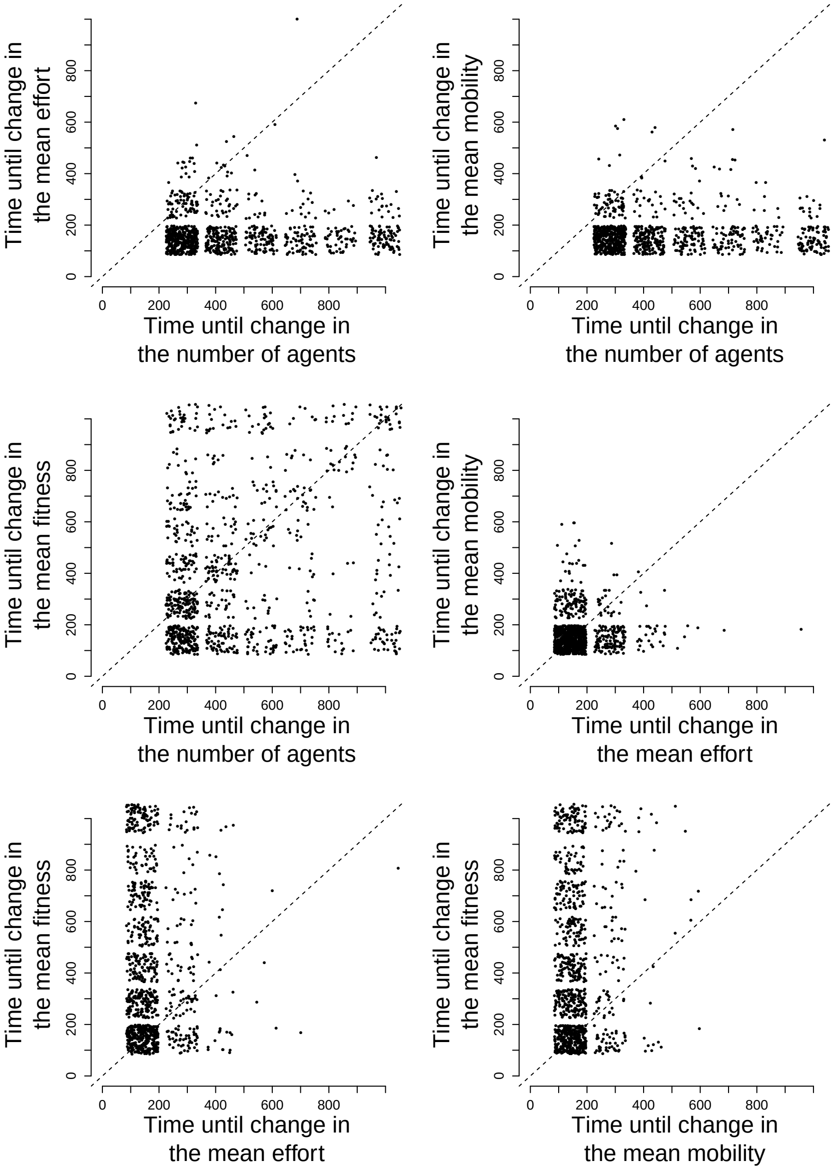


Figure 6.22: Pairwise scatter plots of the number of iterations until there was a significant change in four outcomes – number of agents, mean effort, mean mobility and mean fitness. Using the data from all 1000 simulations. The dashed line shows where these are equal.

6.5 Discussion

By running the model many times with different parameter values I am able to assess how environmental (and other) variables can affect the evolution of mobile foragers. I can also find how certain outcomes of the model evolved over time and how they are impacted by environmental variability.

6.5.1 Simulation Outcomes

When I varied all 12 parameters most of the simulations had either low final mean strategies or high final mean strategies. When I fixed 8 of these parameters and only varied 4, there was the additional frequent simulation type of low mobility and high effort. This was because the default parameters chosen based on the data promoted more low mobility and high effort simulations – which (with the exception of ϕ) can be seen in Figure 6.5b.

If a simulation has low final mean strategies (SA simulations), it will also tend to have the highest numbers of agents, the lowest fitness, low foraging quality and high farming quality. Conversely, if a simulation has high final mean strategies (MF simulations), it will have the lowest numbers of agents, the highest fitness, high foraging quality and low farming quality. Compared to MF simulations, for the low mobility and high effort simulations (SF), the number of agents is slightly higher, fitness is lower, and foraging quality is higher.

The relationships between effort strategy and foraging and farming qualities are intuitive. If there is a lot of foraging then there will be little farming, so q_a will be low. q_f is high because the number of agents able to be supported at a site is low (since too many agents would deplete the foraging resource and die due to low fitness). Hence a natural carrying capacity is found in the model. Since foraging quality depletion is greater if the agents are sedentary foragers (and thus there is less chance for site regrowth), the SF set only occurs when the decay rate, λ, is particularly low. Farming increases the farming quality, and it also has a negative impact on the foraging quality (the farming interference aspect).

In this model it seems that sedentary farming is also associated with low mean fitness and high numbers of agents. These two outcomes are dependent in that more agents mean that resources need to be shared more widely, but also counter-intuitive since low fitness means the probability of fissioning is lower.

As in Chapter 5, the exponentially decreasing relationship between mobility and population density (in Figures 6.6 and 6.9) replicates what is seen in Kelly's (2013) hunter-gatherer mobility data (see Section 2.5.1). Furthermore, the relationship between sedentary farmers, high population densities and decreased fitness also fits with the archaeological record (namely the Neolithic demographic transition Bocquet-Appel (2011a) and evidence for a health decline Lambert (2009) – see Section 1.1.3).

6.5.2 Parameter Sensitivity

Some of the parameters were significantly correlated with various outcomes of the model. Many of these correlations were obvious, and others will have been because of indirect effects. For example the farming decay rate, δ, was negatively correlated with the farming quality (more decay, worse quality); the cost of movement, η, was negatively correlated with the final mean mobility strategy (more movement cost, less movement); the maximum number of foragers, n_{max}, was negatively correlated with fitness (more agents, more people to share resources between).

I used the FIO method to look at parameter distributions in the four extreme strategies (Figures 6.5b and 6.12b). This analysis allowed me to find which parameters were insensitive to outcomes, and for those which were sensitive I could see their effect.

When varying 12 parameters in Experiment 1, the strategy conservatism parameters, κ_m and κ_e, did not have much effect on the outcomes. I take this result as an indication that when strategies evolve they do so via selection rather than random drift. Since all agents start with high mobility and effort strategies it is necessary that some variation is introduced into the population in order for low strategies to evolve – hence when the mutation rate, μ, is very low the simulations do not change much from their initial state (i.e. MF simulations). I disregard the result for the lowest effort and highest mobility simulations from this discussion since they were actually very spread in the values for their strategies.

The number of farmers which can be supported in the model (which is positively affected by both ϕ and n_{max}) promotes low strategy (SA) simulations. However, I also find that parameters which would increase the numbers of agents, p_{max} and ρ_{init} are relatively low in SA simulations. These findings might suggest that large numbers of agents do not encourage sedentary farming, but rather the potential to have large numbers is a prerequisite and an outcome of sedentary farming. This could be because in the process of evolving from a mobile forager the first step (whether it be becoming a farmer or becoming sedentary) discourages large numbers of agents.

Since all simulations started from having a high mobility value it makes sense that the value for η is quite low for all the simulation types – otherwise the agents may have all died due to movement costs. The initial population density, ρ_{init}, also tends to be low in all the simulation types. This could be because high initial population sizes could cause strains on the resources. It is also the case that since there is only one seed agent, having a low initial density makes the impact of this one seed agent stronger. Contradictory to this, the lowest initial densities are seen in the simulations with the highest strategies.

When I varied only the four environmental parameters in Experiment 2 I found stronger, but similar, correlations between parameters and outcomes. The relationship between λ and the final mobility strategy was particularly strong. For the sedentary farming (SA) simulations I find good environmental conditions – high foraging growth rates, low foraging depletion and farming decay rates, and relatively low farming interference effects. For sedentary foraging (SF) simulations I find the best foraging environmental conditions – high foraging growth rates and the lowest foraging depletion rates, I also find that the farming interference effect is high and the farming decay rate is high. These last two findings are unusual; since there is little to no farming it should not matter what the farming decay rate or the farming interference effects are. My interpretation of this result is that the SF simulations are simply the simulations which had very good conditions for reduced mobility, but lacked the right conditions for farming to occur. For high strategy (MF) simulations, the foraging environmental conditions are quite poor, but there are also some farming decay effects (δ is never very small). For these simulations agents can get by by moving often and keeping low numbers of agents, but there is no drive to switch to farming.

High mobility and low effort strategy (MA) simulations have the worst conditions for foraging – low foraging growth rates, high foraging depletion and high farming interference effects – they also have the lowest farming decay rates. Hence, for these simulations agents can grow food quickly via farming, and keep moving from site to site.

When the farming decay rate, δ, is low then farming will evolve in the model (seen in Figures 6.5b and 6.12b). The other parameters differ in their distributions for MA and SA simulations, suggesting that the values for these affect whether high or low mobility evolves. It seems that the evolution of high mobility and farming (MA) will be in response to the worst foraging conditions and the best farming conditions, and for low mobility and farming (SA) to evolve the environmental conditions are good (but not the best) for foraging *and* farming.

When farming does not evolve, the foraging growth rate (r) is not very low. For MF simulations the values for the farming interference parameter and the farming decay rate are quite spread – which makes sense since if there is no farming these effects do not do much. However, for the evolution of SF simulations there does seem to be an association with high farming interference effects and high farming decay rates. It is also the case that SF simulations have the lowest values for the foraging depletion rate (λ), but MF simulations have higher values. Thus, for the evolution of MF simulations the foraging conditions will not be very good for both the foraging and farming environments. For the evolution of SF simulations foraging conditions are the best, and farming conditions are the worst.

6.5.3 Variability

In Experiments 3 and 4 I looked at the effect of temporal and spatial environmental variability on the emergence of different strategy values.

Even though temporal variation was random, and thus the environment had the potential to be in various states, Figure 6.14 shows that the number of simulations with low mobility (SA or SF) decreased when there was temporal variation (there are no MA simulations in these runs of the model, so I will not comment on these.). This may be because MF simulations can occur in a range of different environmental conditions (see Figure 6.12b), but SA or SF simulations tend to need more particular environmental conditions to evolve. Therefore, variation means that although these particular conditions may be met more often (in the random walk), they may still change year on year. It is also the case that SF simulations are only seen when the temporal variation is low (WD is small). When temporal variation is higher SA simulations can still evolve, but most are MF simulations. It may be the case that temporal variability means that it is too risky for foragers to evolve reduced mobility (since foraging quality depends upon 3 parameters), but it is less risky for *farmers* to evolve reduced mobility (since farming quality depends on one parameter and benefits from staying at one site).

When I introduced spatial variability (see Figure 6.16) I found different distributions of final mean strategy values. When there was non-structured spatial variability (spatial heterogeneity) there were no MA or SF simulations – perhaps suggesting that spatial *homogeneity* (even if the environment is of a poor quality) seems to promote mobile foragers becoming either sedentary or farmers, but not both at the same time. When there is structured variability in λ I find less SF simulations. This might be because there are not enough sites with low values of λ to promote SF simulations (in Figure 6.12b I showed that it was the lowest values for λ which gave rise to SF simulations).

Similarly when there is structured variability in δ there are less SA and MA simulations – perhaps because it is only the lowest values for δ which allow farming to evolve. Thus structured and non-structured spatial variability can mean that there are not enough sites with the ideal environmental conditions for certain strategies to evolve – there needs to be the same environmental conditions everywhere for some of the extreme strategies to evolve.

6.5.4 Events Over Time

In Experiment 5 I looked at how simulations evolve over time to allow me to find the order in which events occur. Although the sample size is small, the MA simulations (in red in Figure 6.17) follow similar trajectories over time to the SA simulations, and I hypothesise if given more iterations these simulations may have become sedentary. The MA state thus seems to be a necessary transitional state in some circumstances. Thus, I suggest there are three stable states in my model – MF, SF and SA.

I looked more specifically at how SA simulations evolve. I found that SA simulations become either sedentary before farming (53% of the time), or farm before becoming sedentary (47% of the time) – they do not co-occur. I also found that the SA simulations evolving via becoming sedentary first have the lowest values for the foraging depletion rate, λ, and higher values for r (i.e. when the foraging environment is good); whereas those which become farmers first tend to have the lowest values for the farming decay rate, δ (i.e. when the farming environment is good) (see Figure 6.19c). Hence, the foraging environment is particularly good for SF simulations, bad for MF simulations and moderate for SA simulations. For SA simulations to develop via becoming farmers first the farming conditions will be very good, and for SA simulations to develop via becoming sedentary first the farming conditions will be moderate.

I found that when SA simulations became sedentary before farmers there is one population size increase (see Figure 6.21). When SA simulations became farmers before becoming sedentary there was one increase in population size associated with becoming farmers, and then another increase when they became sedentary. Both of these trajectories still lead to the same carrying capacity for numbers of agents.

When applying my algorithm to look at the order of events (see Figure 6.22 and Table 6.5) I found that in the evolution of SA simulations (with final mean strategies of < 0.5) both strategies become lower and then the number of agents increased. This was true for both pathways of evolution (via sedentism first or farming first). Although this seems to contradict the previous result, it must be remembered that the algorithm detects the first instances of changes. Thus it would not necessarily be the case that sedentism and farming had fully occurred before the number of agents increased; rather that the strategies had first started to change before the number of agents did.

In summary, I think the two pathways of evolution of SA simulations are as follows. First if the conditions are particularly good for farming (δ is low) the agents start to farm more, this also makes foraging quality worse (because of the farming interference effect), so quite quickly agents become farmers. At this point their population increases since farming can support more agents than foragers. There is little benefit to moving since there is no need to seek out non-depleted foraging environments, and thus sedentism evolves. After this another population increase can happen since the lack of movement costs mean agents have higher fitnesses and thus less death and higher fission rates. Alternatively, if the conditions are good for foraging (λ is low) and not too bad for farming, the cost-to-benefit of movement is reduced and thus mobile foragers become less mobile. Since population sizes are low and farming quality is increased with more farming investment, it is only after sedentism occurs that there is selection for agents to farm more.

6.6 Conclusion

In this chapter I have looked at the effect of adding the ability for agents to choose their subsistence strategy. This model replicates the link between increased population size, sedentism and low fitness in farming populations seen in the archaeology evidence (see Section 1.1.3).

In Section 6.2 I showed how there are three main outcome types: ones with relatively low numbers of agents, high effort and mobility strategies, high foraging quality and low farming quality (MF simulations); ones with slightly higher numbers of agents, high effort and low mobility strategies, lower fitness, high foraging quality and low farming quality (SF simulations); and ones with very high numbers of agents, low effort and low mobility strategies, very low fitness, low foraging quality and high farming quality (SA simulations). The differences between MF and SF simulations are comparable to Type A and Type B simulations from the Forager Model. I also found some high mobility, low effort simulations (MA simulations), but these were much rarer than the other three.

I also showed how some parameters are correlated with outcomes of the model. The potential for large numbers of agents at a site was predicted to be a prerequisite to agents becoming sedentary farmers, but actually having large numbers did not encourage sedentary farming. Strategy conservatism made little difference to the model outcomes.

I found that changes in mobility and effort strategies were affected by the environmental conditions. Mobile foragers would become less mobile if the foraging environmental conditions were very good (quite high foraging growth rates and very low foraging depletion rates), the farming environmental conditions were bad (farming decay rates were high) and any farming would negatively impact the foraging quality. Sedentary farming could evolve if both the foraging and farming environmental conditions were good, although the conditions were not the best they could be. I showed that SF simulations are the ones where the foraging conditions are particularly good, allowing reduced mobility to occur, but the farming conditions are not good enough for farming to be a more beneficial strategy.

In Section 6.3 I introduced environmental variability into the model. I found temporal variability discouraged changes in strategies and thus most agents remained mobile foragers. When I introduced spatial variability I found less sedentary farming evolved than when there was no spatial variability, but there were still some changes in the strategies. For non-structured spatial variability (random conditions over the region) I showed that farming and sedentism will evolve at the same time (rather than one at a time as in the no-variability model).

When I looked at how the model changes over time in Section 6.4 I found that sedentary farming simulations evolved from mobile foragers by either first becoming sedentary and then a farmer, or first becoming a farmer and then sedentary – they do not co-occur. When farming comes first there is a two-step population increase – one associated with the switch to farming, and the second associated with becoming sedentary.

7

Conclusions

Summary

In Chapter 1 I gave a summary of what is known about the origins of agriculture – when and where it happened, the consequences it had, and how it may have spread. I also discussed how despite many theories, there is no consensus on how and why it occurred. Since sedentism is linked with the origins of agriculture, I also reviewed some of the theories for why there might be changes in forager mobility. In this chapter I also considered how human behavioural ecology can be used as a framework to understand mobility and subsistence changes.

In Chapter 2 I discussed how evolutionary theory, game theory and agent-based modelling can be used to understand human behaviour in general. I then went on to review some existing models for forager mobility and also those for the origins of agriculture. Some of these models provided me with inspiration for the development of a new model, which I felt was lacking from the literature. Next, I discussed the methodological contributions I have made – a method for parameter sensitivity analysis in mathematical modelling (fitting to idealised outcomes, FIO), an algorithm for predicting when model outcomes change, a method to measure convergence in simulation outcome distributions, and a method to infer parameter-outcome associations and simulation outcome types (the Outcome Clustering method). I then discussed and analysed the ethnographic, archaeological and climate data I have used to help me inform and test my model.

These first two chapters provided the motivation, relevant background literature, tools, and a discussion of data, for Chapters 3, 4, 5 and 6, where I went on to develop and analyse evolutionary models for the origins of agriculture.

In Chapter 3 I replicated an existing game-theoretical model which looks at property rights and subsistence strategies – the model published by Bowles and Choi (2013). I applied the fitting to idealised outcomes method to this model to reveal new insights into its behaviour, and the origins of agriculture.

The behavioural decisions people make will be partially in response to their environment, and also the environment will change in accordance with the behaviour of the people living there. Furthermore, the relationship between population size, mobility decisions and subsistence decisions are all crucial in understanding why and how agriculture first began. Thus, in a human behavioural ecology and niche construction framework, I built an evolutionary model to study the relationships between population growth, farming and reduced mobility. The first stage in this model's development (the Forager Model) which considers mobility decisions of foragers, is explained in Chapter 4. Section 6.1 gives the details of how subsistence strategies were added to the Forager Model to develop the final model; the Forager-Farmer Model model. Hence this final model concerned the evolution of two types of behaviour – mobility and subsistence decisions.

Chapters 5 and 6 discuss the results from the Forager Model and the Forager-Farmer Model. Along with the results from Chapter 3, I will give key findings from these models in the next section. I will specifically discuss if my findings can be validated by data, if they match the results of the models reviewed in Section 2.3, or if they simply make new predictions. In Section 7.2 I will discuss the limitations of this work and in Section 7.3 I will discuss how the Forager-Farmer Model could be used in further work.

7.1 Thesis Conclusions

7.1.1 Property Rights and Subsistence Strategy Changes

Key findings from my replication and analysis of the Bowles and Choi model in Chapter 3 were that for the emergence of farming in the model certain conditions were preferred, these were; group structuring (lots of small groups which do not change much), small (but not too small) group sizes, conservatism (low behavioural experimentation), and farming-friendly property rights. I also found that the productivity of farming does not necessarily have to be less than that of foraging for farming to emerge. Furthermore, the migration rate was unimportant for the emergence of farming.

The work in this chapter also provided an example of how parameter interactions, sensitivities, and complexities, can be missed when using a fix-all-but-one parameter sensitivity analysis. By using the FIO approach I was able to explore many more of these model behaviours.

7.1.2 Mobility Changes in a Forager Population

After running experiments with my own evolutionary model in Chapter 5 I predicted that a reduction in hunter-gatherer mobility was more likely to occur when there were large carrying capacities, large initial population densities and low movement costs. The amount of strategy experimentation was unimportant, as was having a high maximum probability of fissioning.

Temporal variability discouraged the evolution of low mobility, and spatial variability allowed the co-occurrence of both high and low mobility in the same simulated world. The former result matches the archaeological record in SW Asia, where there is a correlation between the climate becoming more stable (at the end of the Late Glacial Maximum, and at the start of the Holocene) and the appearance of sedentism. It is also similar to the model prediction of Dow and Reed (2015) where in bad weather with high variance there is increased mobility and vice versa.

For the evolution of low mobility in my model I found that the foraging growth rate should be high and the depletion rate should be low (i.e. the foraging quality is good). This reflects what is found in Kelly's (2013) ethnographic data (see Section 2.5.1), where in areas of low primary biomass (i.e. where there is more to eat) there are less residential moves. There was no explicit relationship between the foraging quality parameters and mobility behaviour, and thus this result is emergent. This result is also similar to one of the findings from the model by Hamilton et al. (2016); where changes in subsistence ecology (specifically increases in biodiversity) would cause switches to sedentism.

In this chapter I also used the Outcome Clustering method (described in Section 2.4.4) to group the types of outcome that can occur. Using this I found that there was a continuum of outcome types; from those with high mean mobility strategies, high mean fitness, low numbers of agents and low mean foraging qualities, to those with low mean mobility strategies, low mean fitness, high numbers of agents and high mean foraging qualities. Furthermore, I used the algorithm described in Section 2.4.2 to predict the point at which outcomes begin to change significantly in time; I found that if mobility decreases it will do so before there is an increase in the numbers of agents.

It is worth noting that whilst the simulations using the Forager Model started with all agents having random strategies, agents in the Forager-Farmer Model start being mobile foragers. Thus, in the Forager-Farmer Model there is almost no variation in strategies initially, so there needs to be some mutation in order to introduce this. In the

Forager Model having a high initial population density was important for the evolution of reduced mobility. However, in the Forager-Farmer Model this parameter was preferred to be at a low value. This will be because there was only ever one seed agent (an agent with slightly lower mobility and effort strategies than the rest of the population) in the Forager-Farmer Model, regardless of initial population density. Thus for any evolution of sedentism or farming it is beneficial for this seed agent to be at a higher proportion of the population (which will be achieved with lower population sizes).

7.1.3 Mobility and Subsistence Strategy Changes in a Mixed Population

My results from experiments using the Forager-Farmer Model in Chapter 6 showed that three strategy types could evolve in the model; mobile foragers, sedentary foragers and sedentary farmers. Although I do find some mobile farmers, I predict that given more time these simulations would have evolved decreased mobility. I find that with the evolution of sedentary farmers the two strategies evolve in two stages, i.e. mobile foragers becoming sedentary and then farmers, or mobile foragers become farmers and then sedentary. These pathways occurred in roughly equal proportions. The archaeological record does not give a consensus on whether sedentism caused a switch to farming or vice versa (see Section 1.1), and thus in some way validates my result.

There are also relationships between the fitness and population sizes of these strategy types. Mobile foragers have the highest fitness and lowest population size, sedentary foragers have slightly higher numbers of agents and lower fitnesses, and sedentary farmers have the highest population sizes and the lowest fitnesses. This result is not obvious. On the one hand the fitness of agents is the sum of the foraging and farming yields, and these yields decrease if there are many agents at a site. Hence, it might be expected that population size and fitness are inversely related. But on the other hand, for population sizes to increase there needs to be more fissioning than death, but in agents with low fitnesses the opposite would be expected (lower probabilities of fissioning and more death). I hypothesised that since mobile foragers live in the worst environments, only the very fittest can survive. For less mobile agents the conditions are better and thus more agents can be supported at lower fitnesses.

I find that the environmental variables strongly influence the evolution of agents over time. Although the space limitation parameter (the negative effect of farming on the foraging quality) and the foraging growth rate influence the outcomes, the most predictive are the foraging depletion rate and the farming decay rate (λ and δ respectively).

I find that mobile foragers will stay as mobile foragers (even when there is a non-zero mutation rate) when both the foraging conditions are bad (low growth rates and high depletion rates) and the farming conditions are not particularly good either. When there is evolution to sedentary foraging, the conditions are the best for foraging (the lowest foraging depletion rate) and the worst for farming (the highest farming depletion rates). Conversely, when evolution to mobile farming occurs the conditions are the worst for foraging and the best for farming. I have shown that from mobile farming sedentism can then evolve. When sedentary farming evolves from mobile foraging via becoming sedentary first, the foraging conditions are good (but not the best) and farming is good (but not the best). Hence, if the foraging environmental conditions are particularly good, farming may never evolve. There will be a switch to sedentary foraging, but there is no driver for agents to evolve farming. This could be the case in Japan where perhaps the good foraging conditions and not particularly good farming conditions led to semi-sedentary and large forager populations (Bleed and Matsui, 2010).

My analysis showed that if there is an increase in the number of agents and decrease in fitness then these generally happens after decreases in the mobility and effort strategies. I also found that if sedentary farming evolves via agents becoming farmers first then there is a clear two-step increase in the numbers of agents, whereas if it evolves via becoming sedentary first, there is a slight increase in the numbers and then a large increase after the agents become sedentary farmers. Thus, my model predicts that pressures from high population sizes are unlikely to be a driving factor in the evolution of farming; rather high population sizes are something that occur after farming evolves. However, if mobile foragers become farmers and population sizes increase, there could then be less benefits for mobility and thus sedentism could be selected for. In comparison to the models discussed in Section 2.3, Locay (1989) and Dow and Reed (2015) both propose that population pressure could cause sedentism, Locay (1989) and Dow et al. (2009) propose population pressure could lead to agriculture, and Wirtz and Lemmen (2003) predicts population pressure was not a driver for agriculture.

The outcomes of this model replicate to some extent the exponentially decreasing relationship between mobility and population density seen in the ethnographic data (Kelly (2013), see Section 2.5.1). Also, the link between farming, sedentism, high population sizes, and reduced fitness seen in this model replicates what is seen in the archaeological data (reviewed in Section 1.1.3).

In my discussion of the origins of agriculture in Sections 1.1.1 and 1.3.1 I showed that climate change during the Pleistocene-Holocene transition had impacts on how mobile foragers lived. One of these impacts was becoming less mobile and another was starting to cultivate. My analysis of temporal and spatial environmental variability models key components of these climate changes: my temporal variation is equivalent to the more rapid climate fluctuations seen in the Pleistocene (seen in the NGRIP data, Section 2.5.3), and my spatial variation is equivalent to regional variation in which some areas could be refugia. My results indeed show that less temporal variation leads to more sedentism and farming. This refutes the result by Dow and Reed (2011), where climate shocks (which could be seen as similar to temporal variation) were found to induce technological experimentation, which could then lead to agriculture. In terms of spatial variation, I find regional homogeneity leads to the most sedentary farming, but heterogeneity in both the foraging parameters does still lead to some (more so than when there is only variation in one foraging parameter). In the Forager Model I found that structured spatial variability led to the co-occupation of a region by both sedentary and mobile agents, where sedentary agents would stay in the best environments.

7.2 Limitations

In this section I will discuss limitations with the Forager-Farmer Model, and by extension the Forager Model. Limitations of the Bowles and Choi model replication are discussed in Section 3.4.7; and thus I will not repeat them here.

One of the major limitations of this work is in the assumptions of the model. I have tried to base these on informative data, but this was not always available. Assumptions both affected what I chose to include in the model and how I set certain parameter values. I included the factors I believed were most important and interesting in understanding the origins of agriculture, but I am sure there are other factors which are also important. However, with more aspects of human behaviour and the environment added to the model, the more assumptions that need to be made. As the mathematician George Box (1976) put it,

> ... following William of Occam he should seek an economical description of natural phenomena. Just as the ability to devise simple but evocative models is the signature of the great scientist so overelaboration and overparameterization is often the mark of mediocrity.

Therefore, the very nature of modelling means processes will be not included, and caution must be taken when interpreting the model. The assumptions I made in estimating certain parameter values (p_{max}, μ, n_{max} and ϕ) should also be borne in mind. For example, I modelled the relationship between fitness and fissioning probability according to how wealth and reproductive rates are related in the study of Gabbra households by Mace (1996), but perhaps I should have also considered the idea that in wealthy families it may be more adaptive to have fewer children and invest more in them (e.g. Kaplan (1996)). Also, perhaps the assumption that farming quality decreases as soon as a site is unoccupied needs reviewing. This is not the case for the Mikea forager-farmers of Madagascar, who plant crops and then leave the area, returning when the crops are ready for cultivation (Kelly et al., 2005).

A limitation of the FIO method is that there is the risk that I did not run enough simulations to get results which were stable to the effects of stochastic variation in outcomes. In my replication of the Bowles and Choi model I ran the model 1.2×10^8 times, in the Forager Model I ran it 100,000 times for each of Experiments 5, 6 and 7, and I ran the Forager-Farmer Model 10,000 times for Experiment 1 and 100,000 times for Experiment 2. Furthermore, my analysis of the events over time in the Forager-Farmer Model was only based on 1000 simulations. There is no exact way to test how many runs of the model are needed, but generally the more there are the more robust the results are. I am confident that the overall pattern of my results would not change very much if I ran more simulations, but I could possibly give more robust predictions about what the environmental parameter values may be for certain strategies to evolve.

As mentioned in Chapter 2 a lack of detailed data is one of the reasons for creating models, and using the FIO method to analysis parameter sensitivity is one way to not bias results by poorly defined parameter values (if data is lacking). Data is important for testing the validity of the model, and the absence of this is an inadequacy of this work. Ideally, I would have a yearly record of the proportion of farmers to foragers, and how mobile they were, throughout the Pleistocene-to-Holocene transition. With this data I could test how accurate my model predictions were, and thus make strong inferences on what the environmental conditions would have to be for sedentary agriculture to develop when it did. Unfortunately this data does not exist. I do, however, replicate a number of correlations observed in the archaeological and ethnographic literature, and have refrained from making any grandiose statements on the predictive power of my model. Thus, I treat my model results as a means of sharpening intuitions on how generalised environmental states may be in order for certain strategies to evolve.

7.3 Further Work

There are many additional tests and extensions I would like to make to the Forager-Farmer Model. I will describe the main ones in this section.

My model looks at families in a 1000 km^2 region over a 1000 year period. Under particular environmental conditions I found that sedentary farming can evolve during this time. However, in reality (see Table 1.1) the evolution from mobile foragers to sedentary farmers may have taken much longer than this. One of the reasons for this discrepancy is that some of the parameters values I have used are not fixed to real data. However, the results presented in this thesis still have merit – they still give predictions for how the conditions might have been in order for sedentism and farming to evolve, and also the processes in which they occurred. An extension to this work would be to run the model over more iterations, and then analyse the simulations which gave rise to sedentary farming after the number of years it might be expected for the transition from mobile foraging to sedentary farming to occur (this was around 3500 years in SW Asia). This model could then be directly compared to the proxies for agricultural uptake rates and sedentism in the archaeological datasets discussed in Section 2.5.2 (see Figures 2.18b and 2.19b).

In my spatial variability experiments I varied the environmental parameters (the growth rate, depletion rates and space limitation scalar); these parameters directly affect the foraging and farming qualities, which in turn affect the agents living there. The purpose of this was to model differences in the region. Additionally, there could have been other interesting ways to look at spatial variability. One could be to look at the effect of mobility barriers in the region (e.g. mountains and rivers), which could be quite simply modelled by making the cost of movement change at different sites. I could have also looked at more stark differences in the environmental conditions when there is structured spatial variability (rather than the gradual changes I modelled) – this might be similar to the model of the Mimbres region by Anderies and Hegmon (2011). Furthermore, as in the model by Hamilton et al. (2016) it would be interesting to also consider changes in the distance moved (rather than just whether agents move or not) in different region types.

In the Forager and Farmer-Forager Models agents affect each other because of changes they make to the environment and by sharing resources with other agents which occupy the same site. There are no direct interactions between agents. Rather than assuming that people would happily allow others to come and forage at the site they occupy, it would be of interest to include a game-theoretical element of interaction when a new agent tries to migrate to a site. This could be whether the agents fight for the occupation of the site, or perhaps cooperate in defending the site from other migrating agents (similarly to the models of Freeman and Anderies, 2012; Marceau and Myers, 2006). If agents cooperated this could result in the formation of groups of agents – which might be more realistic since nuclear families are not typically alone in their movements or agricultural networks (they would be in foraging bands or farming communities).

I discussed in Section 1.1.3 that storage, property rights and social inequality are all consequences of agriculture. Hence, I could also include the ability for agents to store a certain amount of their resources and, as in Bowles and Choi (2013), allow agents to have a property-rights behavioural strategy whereby stored items might be respected or stolen by agents co-occupying the same site. Since the Forager-Farmer Model takes into account mobility strategies too (and Bowles and Choi's model does not) it would be interesting to look at the relationship between mobility, storage and property rights. All these factors would mean I could then examine social inequality in my model, and investigate the circumstances in which there are consistent differences in the amount of accumulated wealth (from storage of resources, or the regular ownership of a site).

The goal of this thesis was to examine why people switched from foraging to farming during the transition to agriculture. The work in this thesis has tested hypotheses for this, developed a new evolutionary model which could be used to test many more hypotheses surrounding mobility and subsistence behaviour, made explicit predictions that can be tested against archaeological and ethnographic data, and also made several methodological contributions, including a new method for parameter sensitivity analysis in archaeological models.

Appendix

A Data from Robert Kelly

In obtaining the hunter-gatherer data in *The Lifeways of Hunter-Gatherers: The Foraging Spectrum* (Kelly, 2013) I contacted Robert Kelly. Kelly sent me two data tables; the first contains the mobility variables in Table 4-1 of Kelly (2013, pg. 80–84), and the second dataset given to me contains the data in Table 7-3 of Kelly (2013, pg. 178–184).

In the first dataset there were nine discrepancies between the data given to me and the book, for example for the Berens River Ojibwa peoples a figure of 320 was given as the total distance (km) in the book, but in the data given to me this figure was given as the total area (km^2). There were also data entries with vague values given, for example the number of residential moves per year for the Chilkat Tlingit is given as '> 2' and the total area given for the Maidu is given as '455 - 3,255'. I excluded any of the discrepancy data points in my analysis, if a range of values was given I took the mid point, and for data enteries of '> 2' or '2?' I used a value of 2. I copied the Primary Biomass (kg/m^2) values by hand from the book.

The second dataset (Table 7-3 of Kelly (2013, pg. 178–184)) gives the country/area the hunter-gatherer group lives in (e.g. 'Greenland'), the area category (e.g. 'Arctic'), and the population density. There are several discrepancies between the data given to me and the book values, for example for the Anbarra the book gives values of 2 and 43 for population density, and in the database it just gives 43. I use the book value in my analysis, and if there are multiple or a range of values then a mid point is taken.

I also used the data from Table 4-3 in Kelly (2013, pg. 92) on the annual residual moves and the dependence on fish. If an inexact data value was given for residential moves (e.g. '$>$4' or '0-2') the highest value mentioned in the table is given (in the example these would be 4 and 2), and a value of 75 is set when 'High' is given for dependence on fish. Values from tables 7-2 (pg. 171), 7-5 (pg. 195–196) and 7-7 (pg. 201) in Kelly (2013) are used to look at group size, fertility and mortality respectively.

If values in the book are recorded as a range of values I used the mid point value in my calculations.

Table A1 shows the collated mobility and population density data for 87 groups.

Table A1: Collated mobility and population density data for 87 hunter-gatherer groups, from Table 4-1 of Kelly (2013, pg. 80–84) and Table 7-3 of Kelly (2013, pg. 178–184). Some values have been estimated if a vague value was given in the book, or there was a discrepancy between data given to me by Robert Kelly and the published version – explained in the text of this section.

Group	Location	Area Category	Population density (persons/ 100km^2)	Residential Moves per year	Average Distance (km)	Total Distance (km)	Total Area (km^2)	Logistic Mobility (days)	Primary Biomass (kg/m^2)
Anbarra	Australia	Seasonal and wet tropical forests	22.50	3	3.2	7	56	2.5	9.8
Mirrngadja	Australia	Seasonal and wet tropical forests		5	3.5	14.2		1	10.1
Hill Pandaram	India	Seasonal and wet tropical forests	69.60	45	4	144	79.8		3.9
Ainu	Japan	Temperate forests		2	4.3	8.6	171	48	21.5
Agta (Isabela)	Philippines	Seasonal and wet tropical forests		20	5	107			23.6
Mbuti	Africa	Seasonal and wet tropical forests	30.50	11	5.2	57	450		33.1
Nukak	S. America	Seasonal and wet tropical forests		75	5.75	450	450	1	46.2
Guayaki	S. America	Seasonal and wet tropical forests	13.45	50	5.9	295	780		31.6
Aka	Africa	Seasonal and wet tropical forests	28.00	8	7	60	400		25.4
Makah	NW Coast	North American Northwest Coast	86.00	2	7.3	15	923		34.1
Klamath	California	California	25.00	11	7.5	84	1058	27	15.3
Hadza	Africa	Tropical/subtropical deserts	19.50	27	8	216	2520	3.5	11.3
Hadza	Africa	Tropical/subtropical deserts		6.5	11		78		11.3
Penan	Brunei	Seasonal and wet tropical forests		45	8.5	384	861		56.6
Nuuchahnulth (nootka)	NW Coast	North American Northwest Coast	71.50	3	10	30	370.5		34.9
Birhor	India	Seasonal and wet tropical forests	22.00	8	10.3	90.3	130	5.5	13.8
Chenchu	India	Seasonal and wet tropical forests		4	11.2	39.5			15.6
Vedda	India	Seasonal and wet tropical forests		3	11.2	36.3	41		17.2
Semang	Malaysia	Seasonal and wet tropical forests	12	26	11.3	203.8	2475		50.3
Baffinland Inuit	Baffinland	Arctic		60	12	720	25000		0.27
Cheyenne	Plains	Temperate forests	3	33	12	396			6.5
Aeta (Cagayan)	Philippines	Seasonal and wet tropical forests		22	12.8	281.6	3265		26.9
S. Kwakiutl (Ft. Rupert)	NW Coast	North American Northwest Coast	57	4	13.6	35	490		33.6
S. Kwakiutl (Ft. Rupert)	NW Coast	North American Northwest Coast				264			
Siriono	S. America	Seasonal and wet tropical forests		16	14.4	230	780		18.3
Netsilingmiut	Canada	Arctic	0.5	14	16.8	237	6000		0.027
Mlabri (Mrabri)	Thailand	Seasonal and wet tropical forests		24	19	196	2826	1	35.7
Crow (Apsöalooke)	Plains	Temperate forests	2.6	38	19.2	640	61880	32	4.5
Ju/'hoansi (Dobe)	Africa	Tropical/subtropical deserts	10.9	6	23.6	142	1380	10	
_Kade G/wi	Africa	Tropical/subtropical deserts	5	17	25	300	906	10	1.5
G/wi	Africa	Tropical/subtropical deserts	8	11	25	275	782	16	1.5
Other Gulf Salish	NW Coast	North American Northwest Coast		3	34.9	77	631		23.8
Ngadadjara	Australia	Tropical/subtropical deserts		37	43	1600	2600	12	0.6
Micmac	E.Canada	Subarctic/cold forests	2.3		56		3100		17.9
Montagnais	E.Canada	Subarctic/cold forests	4	50	64		2700		7.7

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Group	Location	Area Category	Population density (persons/ 100km^2)	Residential Moves per year	Average Distance (km)	Total Distance (km)	Total Area (km^2)	Logistic Mobility (days)	Primary Biomass (kg/m^2)
Nunamiut	N.Alaska	Arctic	2	10	69.5	725	12350		1.11
Nez Perce	Plateau	Temperate forests	8.9		20		2000		11.3
Kiowa	Plains	Temperate forests	1.4		20				11.4
Ona (Selk'nam)	S. America	Subarctic/cold forests	9	60					8.6
Chilkat Tlingit	NW Coast	North American Northwest Coast	25	2		44	2500		29.6
Bella Coola (Nuxalk)	NW Coast	North American Northwest Coast	11.5				625		30.1
Owikeno Kwakiutl	NW Coast	North American Northwest Coast					639		33.6
Mistassini Cree	E.Canada	Subarctic/cold forests	0.4	10		510	3385		11.9
S. Tlingit	NW Coast	North American Northwest Coast	25	3			1953		29.6
Berens River Ojibwa	Canada	Subarctic/cold forests	4.8			320	320		8.5
Grand L.Victoria Cree	Canada	Subarctic/cold forests	0.7				2890		19.8
Pikangikum (Ojibwa)	Canada	Subarctic/cold forests	3.2				650		8.5
Haisla	NW Coast	North American Northwest Coast	16				4000		32.2
Tsimshian	NW Coast	North American Northwest Coast	57.5	4		370			32
Haida	NW Coast	North American Northwest Coast	79				923		32.9
Quileute	NW Coast	North American Northwest Coast	64.5				190		34.3
Blackfoot (Siksika)	Plains	Temperate forests	4.3		20	20	185		3.9
Quinault	NW Coast	North American Northwest Coast	46				110		34.7
Waswanipi Cree	Canada	Subarctic/cold forests	0.4				4870		12.8
Aleut	Aleutians	Arctic	65	1				32	8.6
Chinook	NW Coast	North American Northwest Coast	148.6				118		35.1
Twana	NW Coast	North American Northwest Coast	25	4		59	211		35.2
Puyallup-Nisqually (S. Salish)	NW Coast	North American Northwest Coast	106.5				191		23.8
Upper Skagit (S. Salish)	NW Coast	North American Northwest Coast	16.8				203		23.8
Squamish	NW Coast	North American Northwest Coast		2		160			18.5
E. Saanich	NW Coast	North American Northwest Coast		4.5		92.5	58		28.8
W. Saanich	NW Coast	North American Northwest Coast		4		243			28.8
Nooksack	NW Coast	North American Northwest Coast					356		28.8
Sanpoil	Plateau	Temperate forests	38	10					5.7
Tasmanians, N.W.	Tasmania	Subarctic/cold forests	14.5			400	376		34.8
Wiyot	California	California	266.5	1			32		19.7
Kidütökadö	Great Basin	Temperate deserts	1.1	40				29	5.8
Tasmanians, S.W.	Tasmania	Subarctic/cold forests	9.3			400	476		34.8
Tolowa	California	California	138	2			91		35.9
Yurok	California	California	155.5	1			35		35
Maidu	California	California	103				1855		6.7
Tasmanians,oyster Bay	Tasmania	Subarctic/cold forests	8			160	572		12
Karok	California	California	98.5				30		18.1
Tasmanians,Big River	Tasmania	Subarctic/cold forests	4.3			480	1114		12

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Group	Location	Area Category	Population density (persons/ 100km^2)	Residential Moves per year	Average Distance (km)	Total Distance (km)	Total Area (km^2)	Logistic Mobility (days)	Primary Biomass (kg/m^2)
Kaibab Paiute	Great Basin	Temperate deserts	3.5				706		3.2
Kua (mobile)	Africa	Tropical/subtropical deserts	2.55	11		990	990	6	2
Walapai	Southwest	Tropical/subtropical deserts	4				588		2.1
Pitjandjara	Australia	Tropical/subtropical deserts						5.5	0.7
Borjeno	Baja Calif.	Tropical/subtropical deserts	37.3					26	1
Aranda	Australia	Tropical/subtropical deserts	3	10			260		0.8
Worora	Australia	Tropical/subtropical deserts	2				743		9.5
Seri	Mexico	Tropical/subtropical deserts	5			248			0.6
Ju/'hoansi (Nyae Nyae)	Africa	Tropical/subtropical deserts						8	2
/Aise (sedentary)	Africa	Tropical/subtropical deserts		0				6	2
Kua (sedentary)	Africa	Tropical/subtropical deserts	2.55	0				26.5	2
Alyawara	Australia	Tropical/subtropical deserts	2.5				1500	7	0.8
Dorobo	Africa	Seasonal and wet tropical forests		6					25.7
Mardudjara	Australia	Tropical/subtropical deserts	0.6					15	0.5
Umpila (Cape York)	Australia	Seasonal and wet tropical forests	40				52.5		9.1
Batak	Philippines	Seasonal and wet tropical forests	54	21.5					30.3
Andamanese (Onge, inland)	Andaman Is.	Seasonal and wet tropical forests		8	2.4	40	8		57.3
Andamanese (coast)	Andaman Is.	Seasonal and wet tropical forests	86				25		57.3
Shasta	California	California	54.05				3255		19.3
Owens Valley Paiute	Great Basin	Temperate deserts	19				1964		1
Washo	California	California	28				2327		4.4
Pume	S. America	Seasonal and wet tropical forests		7	2.1	46	124		0.66

B Corrections to Bowles and Choi's Model

Whilst translating the published description of Bowles and Choi's (2013) algorithm into code I spotted several mistakes and misleading or unclear explanations. Bowles and Choi clarified these over email and the corrections/explanations are as follows:

1. In a Bourgeois - Bourgeois interaction one will win with probability of 0.5.
2. $\theta = -(0.45 - w)/5$
3. Payoffs are reset to zero after each iteration.
4. One iteration = one generation = 20 years.
5. The benchmark parameters for v and γ are 8 and 5 respectively.
6. 'π^S be there average payoff of the group" on page 11 of the supplementary material should be a $\overline{\pi}$.
7. π_i is the average payoff of group i.
8. If the cultural model is chosen to be a sharer (for example), then one sharer will be chosen at random from the cultural model group.
9. An agent could pick itself as its own cultural model.
10. The reward or cost when a civic attempts to punish another individual is shared between all the civics in the group.
11. In the equation for f, n is the size of the group, hence $(1 - \alpha - \beta)n$ is the number of civics in the group.
12. A farmer is picked as a cultural model with probability (frequency of farmers)$^\eta$/(freq. of farmers$^\eta$+freq. of foragers$^\eta$), and similarly for foragers.
13. The number of agents which immigrate into a group is equal to the number that migrate from the group.
14. All the groups are paired for between-group interactions.
15. Any value of θ greater than 1.5 is set to 1.5 (although this has no effect when the benchmark parameters are used).

16. It is not the case that updating will definitely occur if the model's fitness is greater than the updating individual's. What actually happens is the following:

```
if (the model's fitness > the updating individual's)
    $x$ = model's fitness − updating individual's fitness
        if ($x$ < a random number between 0 and 1)
            the individual with update its strategy to the model's strategy
        else
            the individual will not update its strategy
        end
end
```

17. The same set of random numbers are used for each run of 1000 simulations, each of the 1000 simulations have different results though.

C Model Coding and Running Information

All the models presented in this dissertation – my replication of the Bowles and Choi model, and experiments with the Forager model and the Forager-Farmer model – were coded in C++.

Using my laptop (a late 2013 MacBook Pro, with a 2.8 GHz Intel Core i7 processor and 8GB 1600 MHz DDR3 memory) one simulation of the Bowles and Choi model took on average 2.91 seconds, one simulation of the Forager Model experiment 5 took on average 0.084 seconds, and one simulation of the Forager-Farmer model experiment 1 took on average 0.22 seconds.

D Justifying Limit Assumptions in the Bowles and Choi Model

Finding the maximum value for the payoff parameters (C, V_h, τ and z) involved assumptions that were not grounded in observed data. However, in the main analysis (see Section 3.3) it was found that the model outcomes are not very sensitive to the values for C and τ, so there is little evidence to suggest that changing the upper limit of their ranges would make much of a difference.

The parameters V_h and z do have an effect on the model outcome, but I suspected it was their ratio that made the difference, rather than their values individually. If this is true it means the upper limit to these parameter values should not change interpretations in this analysis.

To test this I compared the relative frequencies of parameters in the top 1% of simulations using both the original ranges for V_h and z, and also using half these original ranges (i.e. the top 1% of simulations where $V_h \leq 5$ and $z \leq 9.605$). Figure D1 shows this comparison – I see that the distributions (other than for V_h and V_a, where $V_a = (r - \theta)z - z$) are very similar. Hence, it is really only the value of this ratio that has an effect on the number of farmers in this model, so increasing the upper limit for this should make no difference to our interpretation.

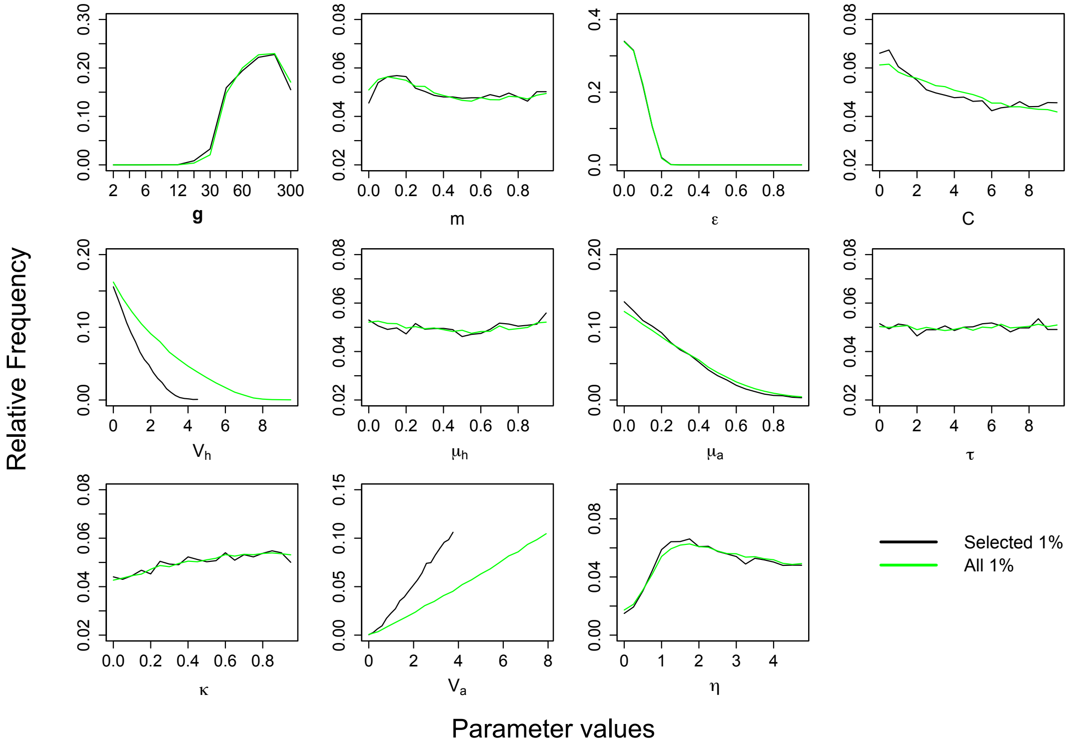


Figure D1: Relative frequency plots of each parameter for the top 1% of simulations (green) and the top 1% of simulations which had both $V_h \leq 5$ and $z \leq 9.605$ (black).

E FIO Ranking Criteria in the Bowles and Choi Model

In my FIO analysis of the Bowles and Choi model, I could have looked at how much farming existed over the period of agricultural establishment to present day, as perhaps simulations which have many farmers at 9000 yBP, but then decrease in number should not be classified as simulations reflecting reality. However, I find a mostly equal trend between the number of farmers at 9000 yBP and the number at 0 yBP, between the number of farmers at 9000 yBP and the minimum number of farmers between 0 and 9000 yBP, and also between the number of farmers at 9000 yBP and the average number of farmers between 0 and 9000 yBP (Figure E1). Hence, I conclude that it is realistic to assume that a simulation will have a similar number of farmers between 0 and 9000 yBP. Thus, my results can be applied to other origins of farming in different regions of the world (as the Near East was the earliest).

I also could have considered the number of bourgeois farmers at 9000 yBP as my acceptance criteria in this analysis. However, I found that out of all the simulations 92.5% were in both the highest 1% number of farmers and the highest 1% number of Bourgeois farmers. Thus the difference this makes to the results in small, which can also be seen in Figure E2.

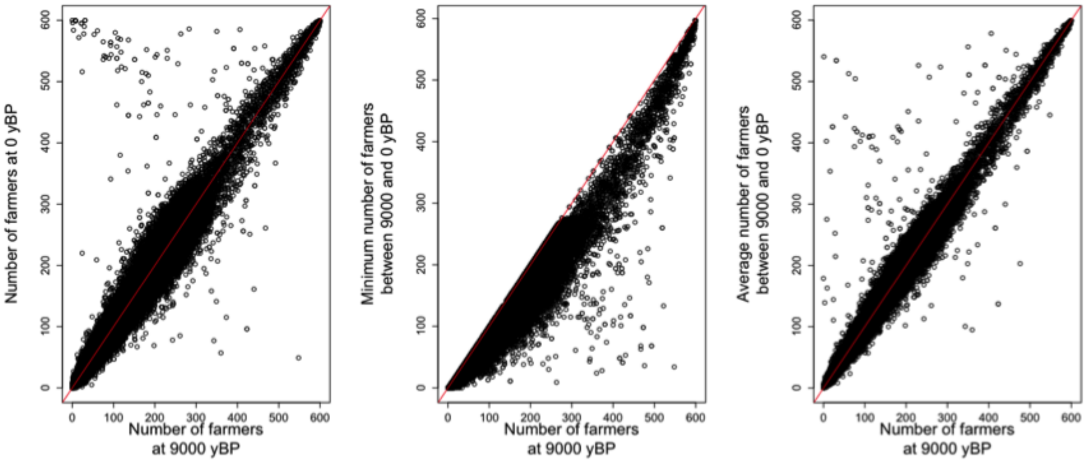


Figure E1: How the number of farmers at 9000 yBP in the model relates to the number at 0 yBP (left); the minimum number between 9000 and 0 yBP (middle); and the average number between 9000 and 0 yBP (right). The line $y = x$ is shown in red.

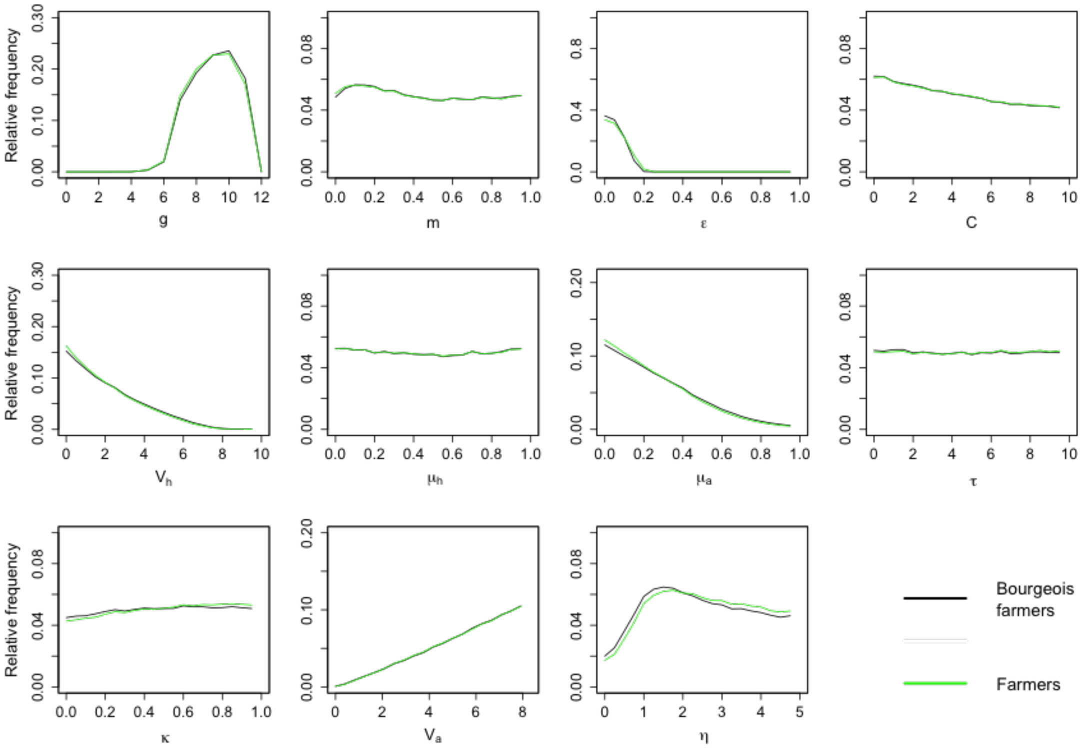


Figure E2: Relative frequency plots of each parameter for the top 1% slices of the 1.2×10^7 simulations. When the number of Bourgeois farmers is used as the success criteria (black) and when the number of farmers is used as the success criteria (green).

F ODD Protocol for the Forager Model

The ODD (Overview, Design concepts, Detail) protocol offers a consistent way to communicate agent-based models with other researchers (Grimm et al., 2010). The Forager Model has been described without this protocol in Chapter 4, but as good practice I will also describe the model using the seven subelements of the ODD protocol here. I will reference parts of Chapter 4 when necessary, rather than repeat myself.

F.1 Purpose

The Forager Model is used to consider the circumstances for which foragers become less mobile, and what consequences and associations this transition might have.

F.2 Entities and State Variables

Entities in the model are families and sites. State variables for families are their fitness, mobility strategy and which site the family occupies. State variables for sites include spatial coordinates and foraging quality.

F.3 Process Overview and Scheduling

Time is modelled as discrete iterations where one iteration represents one year. State variables can be updated each iteration. The flow diagram on page 144 gives an overview of the model.

F.4 Design Concepts

1. Adaptation: Agents in the model can change their mobility strategy via random mutation, and the strategy will change more in this step if the agent is less fit. Fitter agents are also more likely to fission and thus pass on their mobility strategy to the new agent. Thus natural selection acts on the mobility strategy.

2. Emergence: The mobility strategies, fitnesses and number of agents, and the foraging quality of sites over time can all change sometimes unpredictably.

3. Objectives: Agents want to have a high enough fitness not to die.

4. Prediction and Learning: If agents have a high fitness they will not mutate their mobility strategy by much (if mutation occurs). This could be thought of learning or predicting from past experience what mobility strategy might be beneficial.

When agents move site they predict, based on the current conditions, which site will be most beneficial (in terms of fitness) to move to.

5. Sensing: Agents can sense the current environmental conditions of sites in the calculation of which site to move to.

6. Interaction: Agents and the sites they occupy interact with one another via the process of foraging. Agents do not interact with one another.

7. Stochasticity: Initial conditions, fissioning, mutation and movement all have random elements.

8. Observation: At the beginning of each iteration, and at the end of the entire simulation, all state variables can be recorded.

F.5 Initialization

Section 4.6 gives details of the initial state of the model.

F.6 Input data

There is no input data to the Forager Model.

F.7 Submodels

The submodels of the Forager Model (changes in foraging quality and fitness, fissioning, mutation, movement) are explained in detail in Sections 4.1.1, 4.2, 4.3, 4.4 and 4.5 respectively. All constants, variables and parameters in the Forager Model are given in Table 4.1.

G Weighted Selection Algorithm

I use an algorithm to select a value from a list (usually numbers between 0 and 1) weighted on how big the value is. I use this algorithm in a few places in my code, one of which is where I select the new site (*randsite*) a migrating agent will go to based on my calculation of the attractiveness of each of the sites (*siteattract*). This algorithm is as follows

```
// a. Sum all the site attractivenesses:
double sumattract = 0;
for (int s=0; s<NUMSITES; s++)
{
   sumattract = sumattract + siteattract[s];
}

// b. Pick a random number between 0 and the sum
randnum = ((double)(rand() % 1000)/1000)*sumattract; // [0,sumattract)

// c. Go through the items one at a time, subtracting each weight
// from your random number, until you get the item where the
// random number is less than that item's weight

for (int s = 0; s < NUMSITES; s++)
{
   if (randnum < siteattract[s])
   {
      randsite = s;
      break;
   }
   randnum = randnum - siteattract[s];
}
```

H Details of the Forager Model Runs

Table H1: Constants and parameters in the FIO Experiment 1 – to check the effect of initial conditions. Initial conditions are changed 100 times and each combination is ran 1000 times.

Constants		Value
	Number of simulations	1,000 × 100
	Number of iterations	1,000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		Range
r	Foraging quality growth rate	$[0,1]$
λ	Foraging quality depletion scalar	$[0,1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table H2: Constants and parameters in the FIO Experiment 2 – to check how many iterations to run the model for.

Constants		Value
	Number of simulations	1000
	Number of iterations	2000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		Range
r	Foraging quality growth rate	$[0,1]$
λ	Foraging quality depletion scalar	$[0,1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table H3: Constants and parameters in the FIO Experiment 3 – to check the effect of region size. The model is run 1000 times for six different region sizes.

Constants		Value
	Number of simulations	1000×6
	Number of iterations	1000
s_x	Number of sites in x axis	8, 9, 10, 11, 12, 20
s_y	Number of sites in y axis	8, 9, 10, 11, 12, 20
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		Range
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table H4: Constants and parameters in the FIO Experiment 4 – using an average to summarise the final population.

Constants		Value
	Number of simulations	1,000
	Number of iterations	1,000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		Range
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table H5: Constants and parameters in the FIO Experiment 5 – varying all 8 parameters.

Constants		Value
	Number of simulations	100,000
	Number of iterations	1000
	Maximum number of agents allowed	600
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
κ_m	Mobility strategy conservatism	$[50, 150]$
p_{max}	Maximum probability of fission	$[0, 0.5]$
η	Fitness cost of movement per site	$[0, 0.2]$
n_{max}	Maximum number of agents which can be supported at a site	$[2, 6]$
μ	Mutation rate	$[0, 1]$
ρ_{init}	Initial population density	$[0.05, 0.2]$

Table H6: Constants and parameters in the FIO Experiment 6 – varying 4 parameters.

Constants		Value
	Number of simulations	100,000
	Number of iterations	1000
	Maximum number of agents allowed	600
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	$[0, 0.5]$
η	Fitness cost of movement per site	$[0, 0.2]$
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table H7: Constants and parameters in the FIO Experiment 7 – varying 2 parameters.

Constants		Value
	Number of simulations	100,000
	Number of iterations	1000
	Maximum number of agents allowed	600
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table H8: Constants and parameters in the FIO Experiment 8 – looking at temporal variability.

Constants		Value
	Number of simulations	10,000 × 3
	Number of iterations	1000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1
WD	Random walk distance	0.1
	Run-in time	300

Table H9: Constants and parameters in the FIO Experiment 9 – looking at spatial variability.

Constants		Value
	Number of simulations	10,000 × 3
	Number of iterations	1000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table H10: Constants and parameters in the non-FIO Experiment 10 – looking at simulations over time.

Constants		Value
	Number of simulations	1000
	Number of iterations	1000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

I Investigating Mutation Rate

My experiments suggested that the mutation rate did not seem to effect which cluster each simulation was assigned to. To test this further I ran the model with $\mu = 0$ and varied the other 7 parameters (otherwise the same as in Experiment 5), and also set $\mu = 0$ and varied only r and λ (otherwise the same as in Experiment 7). I found that setting $\mu = 0$ gave less high mean mobility strategy outcomes, which can be seen in Figure I1. A comparison of the clustering results when varying 7 parameters were very similar to when μ was varied from 0 to 1 (Experiment 5). Figures I2a and I2b show the outcomes and parameter inputs in the clusters of simulations. A comparison of this figure with Figures 5.8 and 5.12 give little differences.

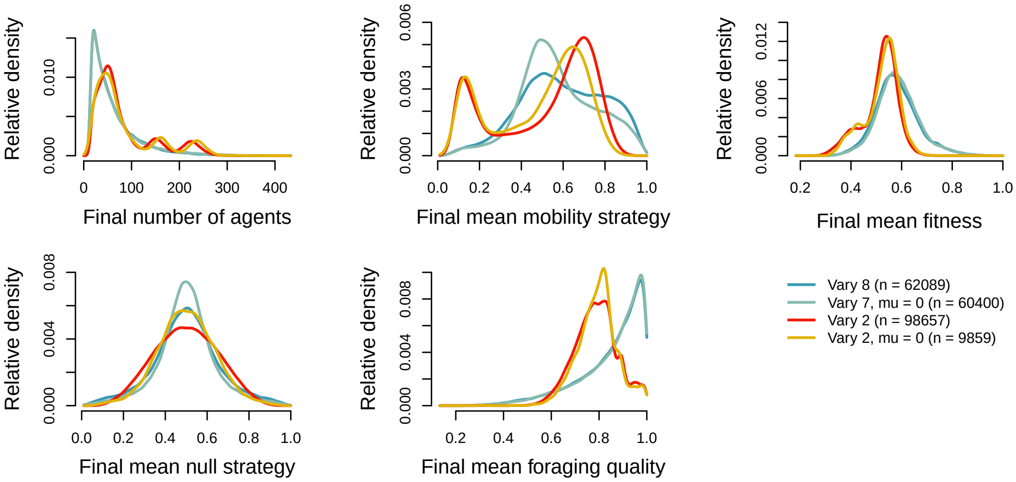
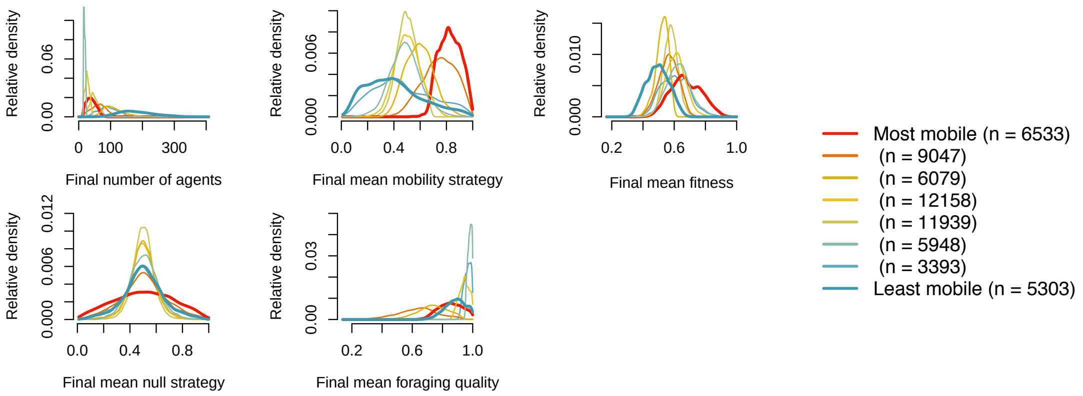
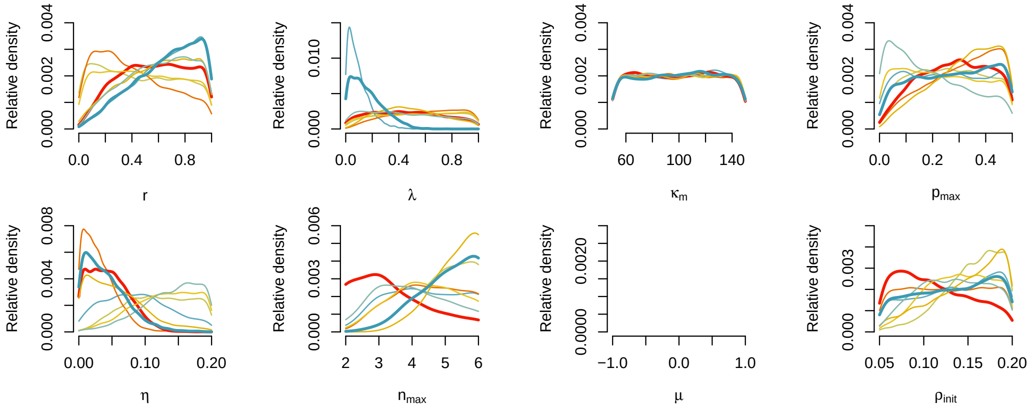


Figure I1: A comparison of the relative densities of simulation outcomes when varying all 8 parameters, when varying 7 parameters and fixing $\mu = 0$, when varying 2 parameters and setting $\mu = 0.04$, and when varying 2 parameters and setting $\mu = 0$ (and unless otherwise stated default parameter values are used).



(a) Outcomes of the different clusters of simulations when seven parameters are varied.



(b) Parameters of the different clusters of simulations when seven parameters are varied.

Figure I2: The outcomes (a) and parameters (b) in the different clusters of simulations when there is no mutation ($\mu = 0$), using all the simulations with ≥ 15 agents alive in the final iteration. The most and least mobile clusters are highlighted with a slightly thicker line.

J When the Environment Becomes Stable

In the main text I look at temporal variability occurring in the model after some run-in period, here I investigate the effect of stabilising temporal variability. To do this I ran the model 1000 times where for the first iteration a random value for r and λ were chosen (all the other parameters were at their default value, see Table J1), and then until iteration 500 r and λ varied according to a random walk with a walk distance of 0.1 (as described in Section 5.4.1). The value for r and λ at iteration 500 was then kept the same until iteration 1000. I compared this to a run of the model where there was no temporal variability, and found little difference in the outcomes – see Figure J1. In fact, the temporal variability in the first 500 iterations appears to make no difference, and the outcome is only determined by which values for r and λ there are at iteration 500. I compare the relationship between parameter values at iteration 500 and the final mean mobility strategy in both the temporal variability and no variability runs in Figure J2.

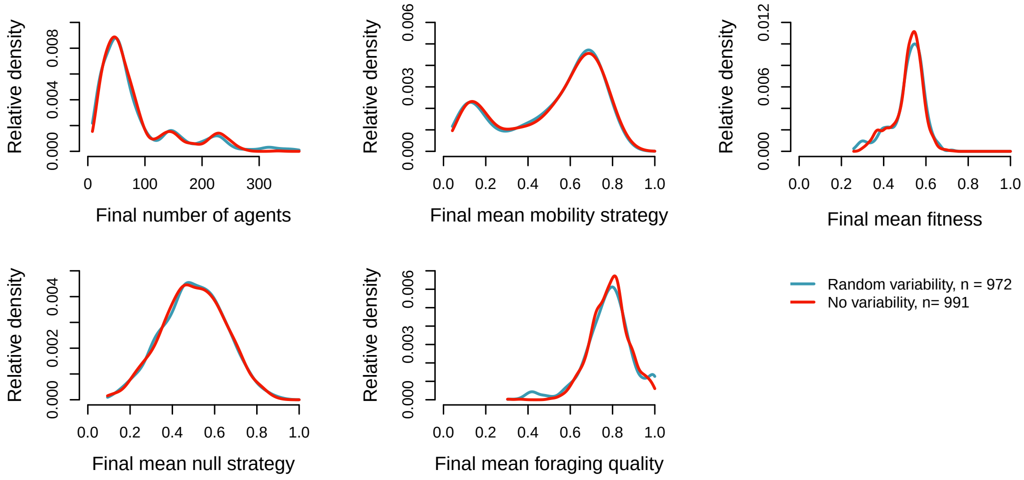


Figure J1: Relative densities of outcomes in the simulations with stabilising random variability (blue) and the simulations with no variability (red). Only simulations with $\geq$ 15 agents alive in the final iteration are included.

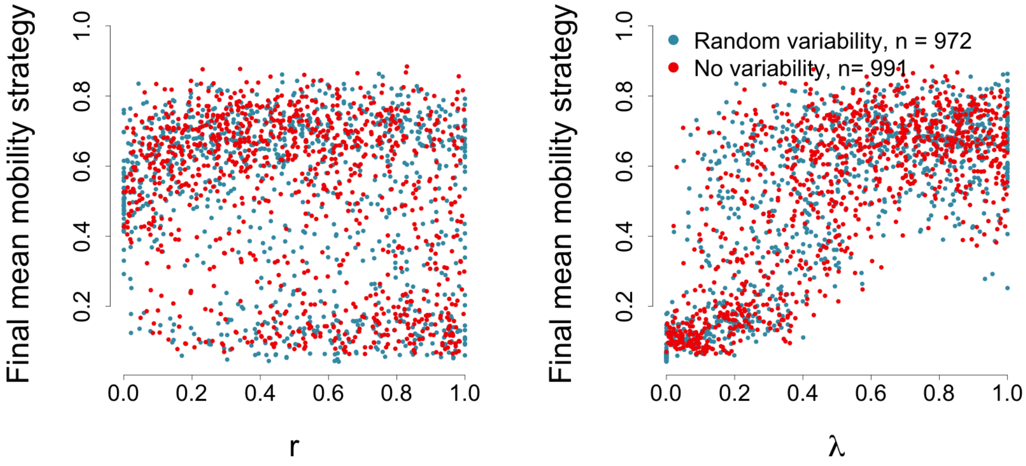


Figure J2: The relationship between parameter values at the 500 iteration (which is the same as any other iteration when there is no variability) and the final mean mobility strategy in the simulations with stabilising random variability (blue) and the simulations with no variability (red). Only simulations with ≥ 15 agents alive in the final iteration are included.

Table J1: Constants and parameters when I look at the switch from temporal variability to stability. This involves running it once with variability on, and once with it off (to compare).

Constants		Value
	Number of simulations	1000×3
	Number of iterations	1000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0,1]$
λ	Foraging quality depletion scalar	$[0,1]$
κ_m	Mobility strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of agents which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1
WD	Random walk distance	0.1
	Run-in time	0
	Iteration of stability	500

K Preliminary Checks for the Forager-Farmer Model

For comparability between adding subsistence strategies to the model and not (i.e. the work described in Chapters 5 and 6 respectively), I set the number of sites, the number of iterations and the minimum foraging quality, equal to their values in the Forager Model (namely 100, 1000 and 0.1 respectively). However, I still perform some checks on these constants to make sure that I understand their influence on the model.

K.1 Number of Iterations

I ran the model 1000 times over 1900 iterations and recorded various outcomes every 100 iterations. Table M1 shows the parameters in this experiment and Figure K1 shows the distribution of outcomes at each of the recorded iterations. I do see changes in the mean value between iterations 1000 and 1900, but from Figure K2 I can see the relative densities of outcomes between iterations 1000 and 1900 are quite similar, and thus my interpretation of the results would be similar.

K.2 Number of Sites

I ran the model 1000 times for 5 different region sizes – 8×8, 9×9, 10×10, 11×11, and 12×12, Table M2 shows the parameter values used in this experiment. In Figure K3 I show the distributions of the final outcomes of the simulations for each of the region sizes. I see that increasing the region size means that there can be more agents in the final iteration and the final foraging quality is higher, but otherwise the outcomes do not change too much.

K.3 Averaging

I ran the model 1000 times over 1000 iterations, varying r, λ, β and δ. I saved all the family and site information in the final iteration, to see whether using mean values is representative of the whole population.

I looked at the relationship between the densities of final outcomes and the mean value calculated for these outcomes. The main concern is finding out whether a mean value of around 0.5 means that the outcomes are all around 0.5, or that they are spread between 0 and 1 (and therefore give an average of 0.5). I find that the latter is often the case for effort, mobility and null strategies, but for the final fitness and the foraging quality the former is often the case. For the farming quality there are very few simulations with a mean outcome of 0.5. These results can be seen in Figure K4, where the

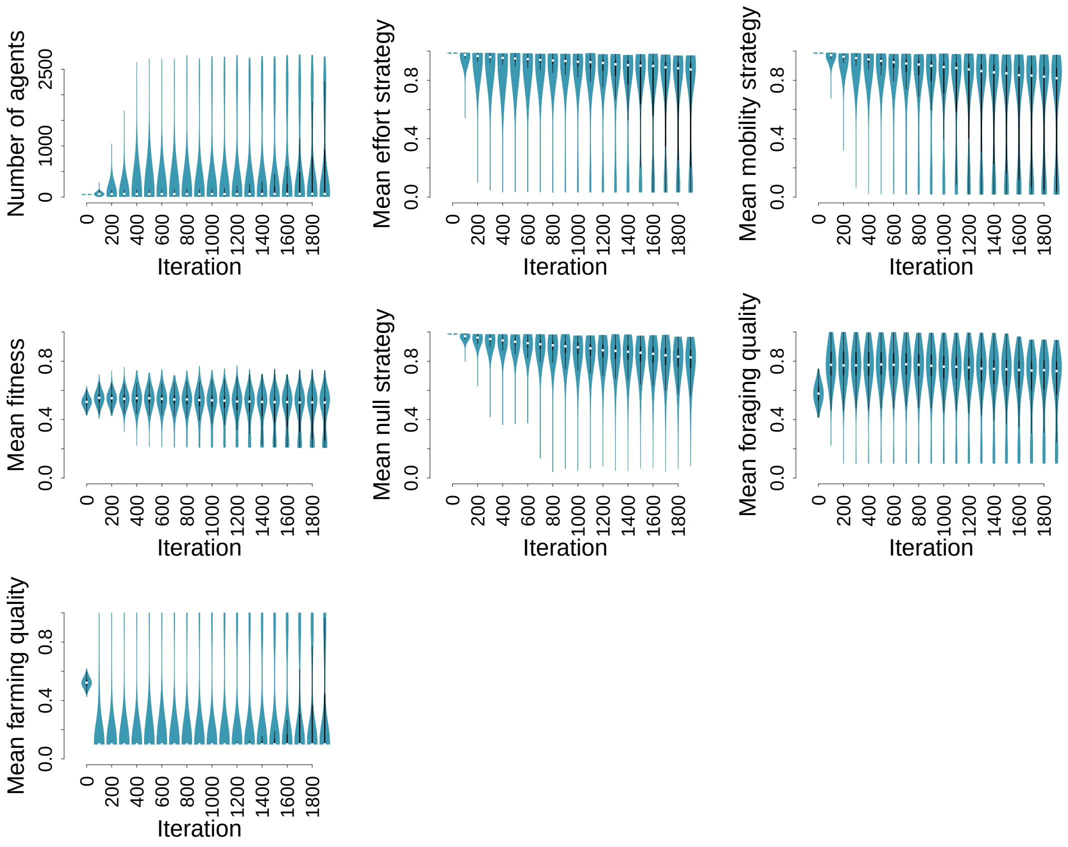


Figure K1: Violin plots of model outcomes at various iterations of 1000 simulations.

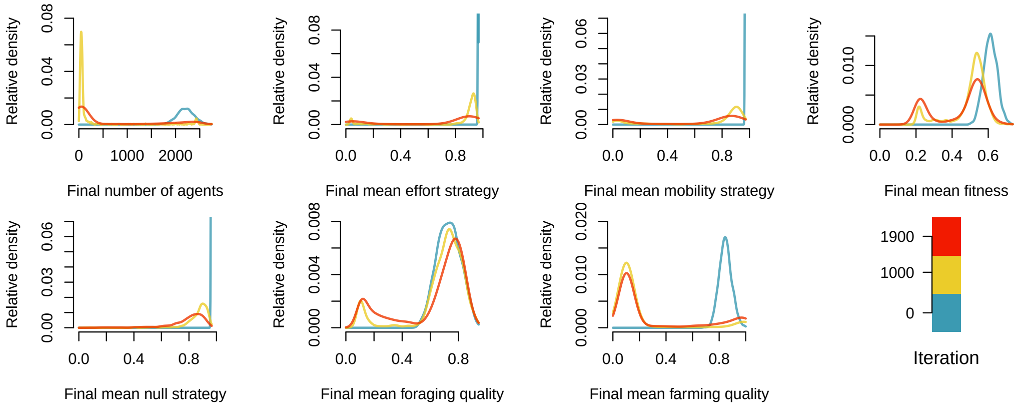


Figure K2: Relative densities of model outcomes in iterations 1, 1000 and 1900.

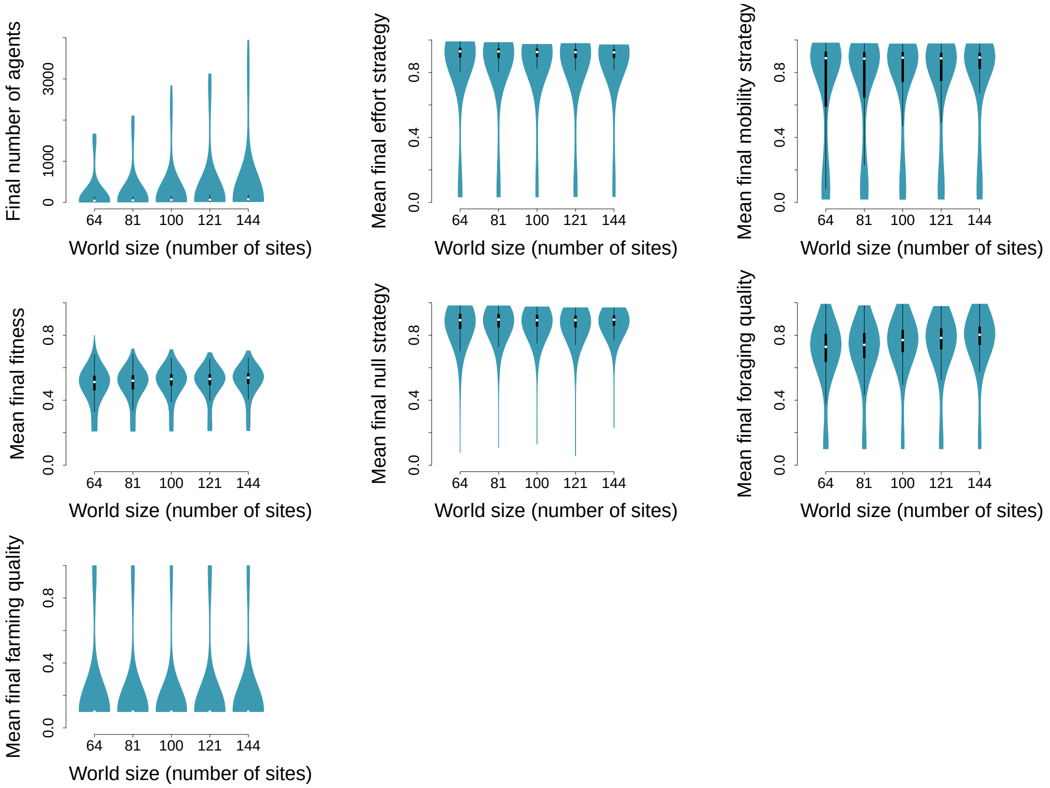


Figure K3: Violin plots of the final properties of simulations for different region sizes.

yellow lines are those with final mean values of around 0.5.

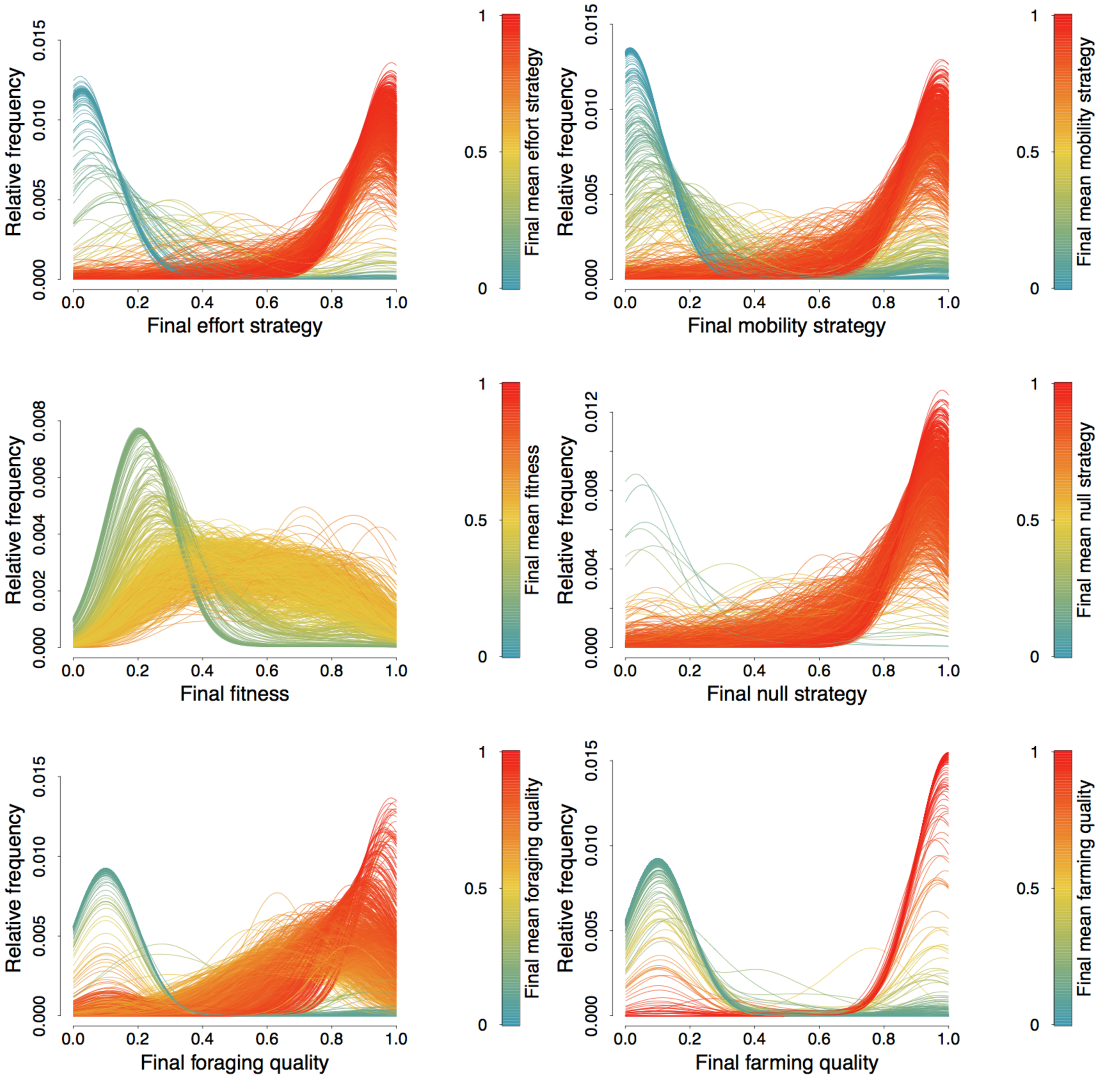


Figure K4: Relative frequencies of all final outcomes coloured by the final mean value.

K.4 Outcomes of Preliminary Checks

In the Forager Model I also looked at the effect from initial conditions, however in the Forager-Farmer Model every simulation has the same initial strategies (0.99 with one seed agent with a strategy of 0.8), so this is somewhat unnecessary.

These preliminary checks have shown that the distribution of outcome values are still changing at the 1000th iteration (i.e. they do not stabilise at this point). Because of this I cannot say whether the outcome types are stable strategies or not – i.e. will there always be some simulations with high mobility and effort strategies, or over time do they all become low mobility and effort simulations? However, this does not invalidate my results, it just means that I need to consider the fact I am only looking at changes over a 1000 year period. For example, rather than using the model to ask “what are the conditions for the evolution of sedentary farming?”, I would instead ask “what are the conditions for the evolution of sedentary farming over 1000 years?”.

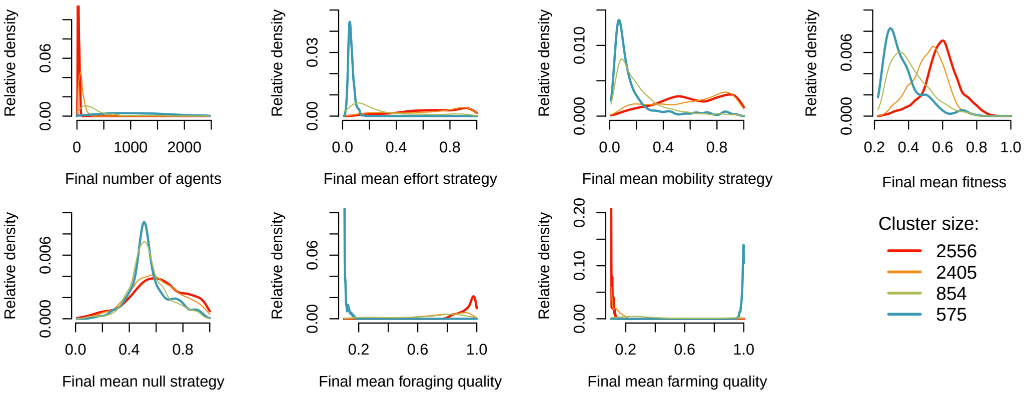
The preliminary checks also show that using a region size of 10 × 10 does not bias results too much, and when a final mean outcome is around 0.5, I need to remember that this means (in most cases) that the final agents have a wide distribution of outcome values (they are not all around 0.5).

L Cluster Analysis Using the Forager-Farmer Model

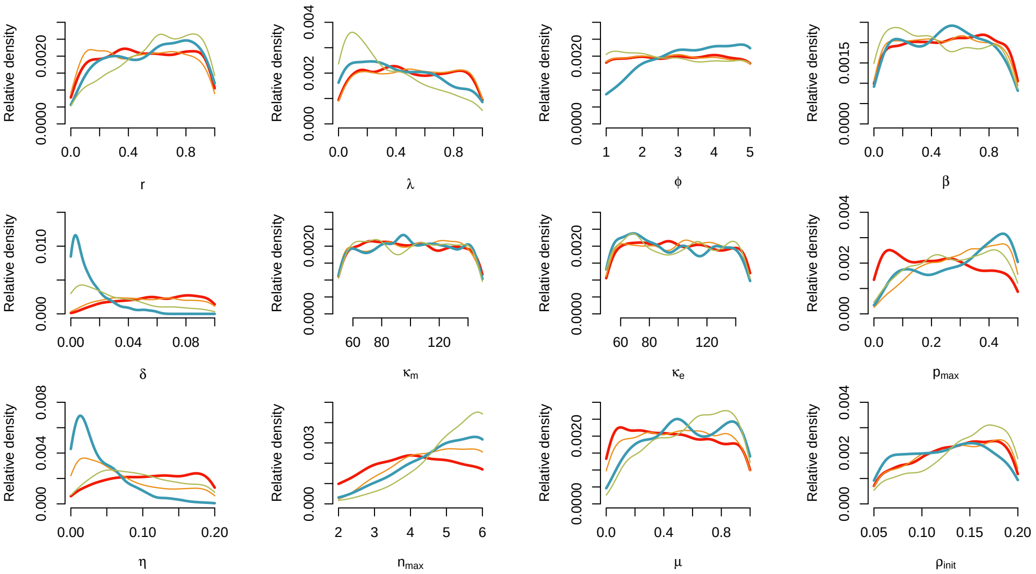
I used the Outcome Clustering method described in Section 2.4.4, namely the function 'Mclust' in the R library 'mclust' (Fraley and Raftery, 2002; Fraley et al., 2012; R Core Team, 2013), to cluster my simulations by the 6 outcomes (final number of agents, mean effort and mobility strategies, mean fitness, foraging quality and farming quality). For Experiment 1, in which I varied all 12 of the parameters, the algorithm found 4 clusters. The relative frequencies of the outcomes and parameters are plotted in Figures L1a and L1b. Pairwise relationships between all the outcomes, coloured by cluster, are plotted in Figure L2.

I will refer to two extreme types of simulation as Type 1 and Type 2. Type 1 simulations have low numbers of agents, high effort and mobility strategies, high final mean fitnesses, high foraging quality and low farming quality. Type 2 have the opposite – high numbers of agents, low final mean effort and mobility strategies, low final mean fitness, low final mean foraging quality, and high final mean farming quality. From my cluster analysis I find a clear Type 2 cluster (in the plots this is the blue cluster). There is less of an obvious Type 1 cluster (red in the plots) where the final mean strategies are generally high, but still quite spread.

Type 2 simulations have the lowest values for δ and η, and the highest values for n_{max}. They also have relatively high values for r, low values for λ, high values for ϕ, high values for p_{max}, high values for μ. The placement of a simulation into any of the clusters is insensitive to the value of β, κ_e, κ_m or ρ_{init}. Hence for the evolution of mostly sedentary farmers the foraging and farming conditions should be good, the decay term in farming should be low, the number of agents should have the potential to be quite big, the cost of movement should be low, and there should not be too little mutation. Interpretation of what influences the evolution (or stability) of mobile foraging is not as clear, because there is no cluster with solely highly mobile foragers.



(a) Outcomes in different clusters.



(b) Parameters in different clusters.

Figure L1: The outcomes (a) and parameters (b) in the different clusters, using all the 6390 simulations with $\geq$ 15 agents alive in the final iteration when all parameters are varied.

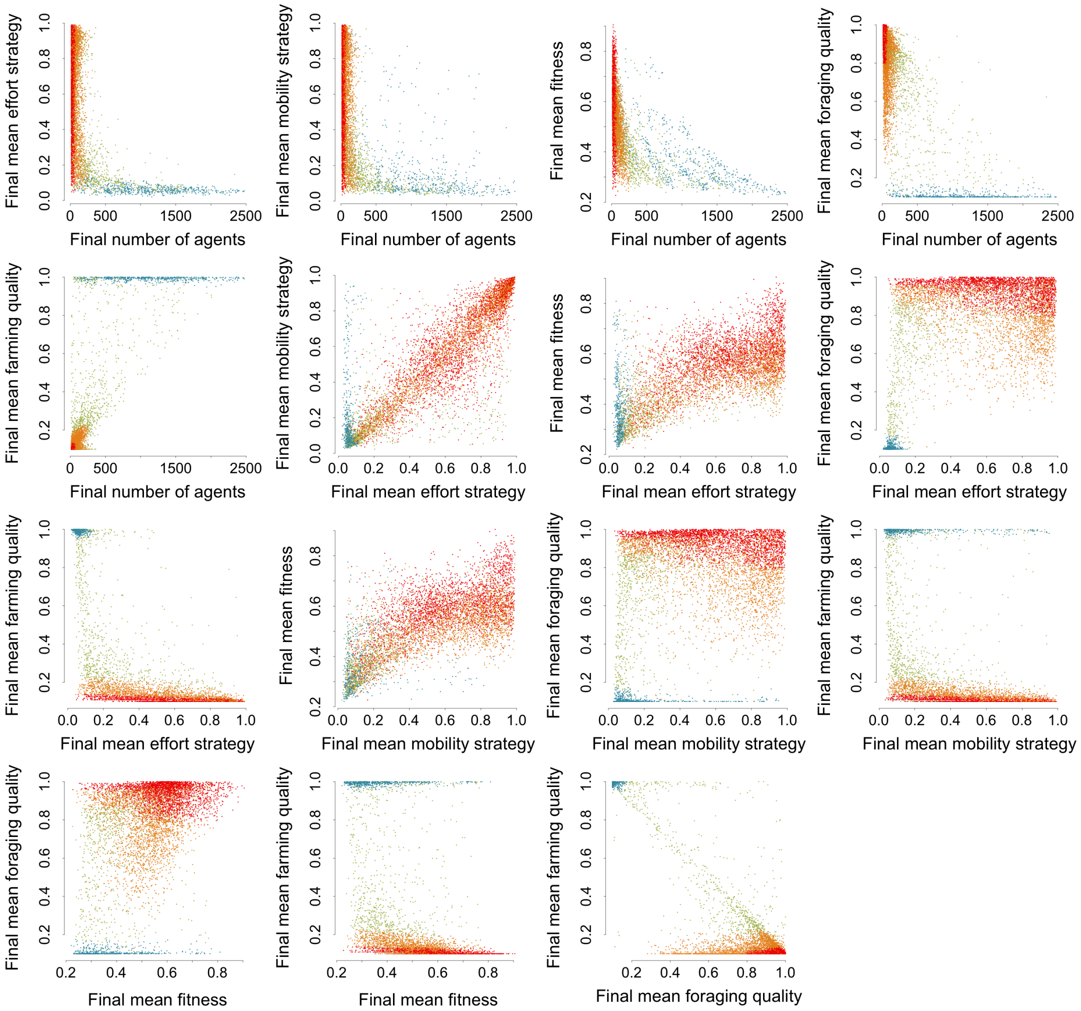


Figure L2: Outcome pairs coloured by cluster, using all the 6390 simulations with ≥ 15 agents alive in the final iteration when all parameters are varied.

M Details of the Forager-Farmer Model Runs

Table M1: Constants and parameters in an experiment to check how many iterations to run the model for.

Constants		Value
	Number of simulations	1000
	Number of iterations	2000
	Maximum number of agents allowed	3000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0,1]$
λ	Foraging quality depletion scalar	$[0,1]$
ϕ	How many times more farmers can be supported than foragers	5
β	Space limitation scalar	$[0,1]$
δ	Farming depletion parameter	$[0,0.1]$
κ_m	Mobility strategy conservatism	100
κ_e	Effort strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of foragers which can be supported at a site	6
μ	Probability of mutation	0.04
ρ_{init}	Initial population density	0.1

Table M2: Constants and parameters in an experiment to check the effect of region size. The model is run 1000 times for five different region sizes.

Constants		Value
	Number of simulations	1000 × 6
	Number of iterations	1000
	Maximum number of agents allowed	1920,2430,3000,3630
s_x	Number of sites in x axis	8, 9, 10, 11, 12
s_y	Number of sites in y axis	8, 9, 10, 11, 12
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0,1]$
λ	Foraging quality depletion scalar	$[0,1]$
ϕ	How many times more farmers can be supported than foragers	5
β	Space limitation scalar	$[0,1]$
δ	Farming depletion parameter	$[0,0.1]$
κ_m	Mobility strategy conservatism	100
κ_e	Effort strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of foragers which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table M3: Constants and parameters in an experiment to check the effect of averaging.

Constants		Value
	Number of simulations	1000
	Number of iterations	1000
	Maximum number of agents allowed	3000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		Range
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
ϕ	How many times more farmers can be supported than foragers	5
β	Space limitation scalar	$[0, 1]$
δ	Farming depletion parameter	$[0, 0.1]$
κ_m	Mobility strategy conservatism	100
κ_e	Effort strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of foragers which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table M4: Constants and parameters in the FIO Experiment 1 – varying all 12 parameters.

Constants		Value
	Number of simulations	10,000
	Number of iterations	1000
	Maximum number of agents allowed	3000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		Range
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
ϕ	How many times more farmers can be supported than foragers	$[1, 5]$
β	Space limitation scalar	$[0, 1]$
δ	Farming depletion parameter	$[0, 0.1]$
κ_m	Mobility strategy conservatism	$[50, 150]$
κ_e	Effort strategy conservatism	$[50, 150]$
p_{max}	Maximum probability of fission	$[0, 0.5]$
η	Fitness cost of movement per site	$[0, 0.2]$
n_{max}	Maximum number of foragers which can be supported at a site	$[2, 6]$
μ	Mutation rate	$[0, 1]$
ρ_{init}	Initial population density	$[0.05, 0.2]$

Table M5: Constants and parameters in the FIO Experiment 2 – varying 4 parameters.

Constants		Value
	Number of simulations	100,000
	Number of iterations	1000
	Maximum number of agents allowed	3000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
ϕ	How many times more farmers can be supported than foragers	5
β	Space limitation scalar	$[0, 1]$
δ	Farming depletion parameter	$[0, 0.1]$
κ_m	Mobility strategy conservatism	100
κ_e	Effort strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of foragers which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table M6: Constants and parameters in the FIO Experiment 3 – looking at temporal variability.

Constants		Value
	Number of simulations	10,000
	Number of iterations	1000
	Maximum number of agents allowed	3000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0, 1]$
λ	Foraging quality depletion scalar	$[0, 1]$
ϕ	How many times more farmers can be supported than foragers	5
β	Space limitation scalar	$[0, 1]$
δ	Farming depletion parameter	$[0, 0.1]$
κ_m	Mobility strategy conservatism	100
κ_e	Effort strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of foragers which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1
WD	Random walk distance	$[0, 1]$
	Run-in time	0

Table M7: Constants and parameters in the FIO Experiment 4 – looking at spatial variability.

Constants		Value
	Number of simulations	10,000 × 5
	Number of iterations	1000
	Maximum number of agents allowed	3000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0,1]$
λ	Foraging quality depletion scalar	$[0,1]$
ϕ	How many times more farmers can be supported than foragers	5
β	Space limitation scalar	$[0,1]$
δ	Farming depletion parameter	$[0,0.1]$
κ_m	Mobility strategy conservatism	100
κ_e	Effort strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of foragers which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

Table M8: Constants and parameters in the non-FIO Experiment 5 – looking at simulations over time.

Constants		Value
	Number of simulations	1000
	Number of iterations	1000
	Maximum number of agents allowed	3000
s_x	Number of sites in x axis	10
s_y	Number of sites in y axis	10
$q_{f,min}$	Minimum foraging quality	0.1
Parameters		**Range**
r	Foraging quality growth rate	$[0,1]$
λ	Foraging quality depletion scalar	$[0,1]$
ϕ	How many times more farmers can be supported than foragers	5
β	Space limitation scalar	$[0,1]$
δ	Farming depletion parameter	$[0,0.1]$
κ_m	Mobility strategy conservatism	100
κ_e	Effort strategy conservatism	100
p_{max}	Maximum probability of fission	0.14
η	Fitness cost of movement per site	0.05
n_{max}	Maximum number of foragers which can be supported at a site	6
μ	Mutation rate	0.04
ρ_{init}	Initial population density	0.1

N Research Article

This appendix contains the work from Chapter 3 published as:

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