Competitive Exclusion, Diversification, and the Origins of Agriculture

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Selected Paper prepared for presentation at the American Agricultural Economics Association


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Introduction

Hunting and gathering was the dominant source of food production for most of human history. In a relatively short interval, however, agriculture emerged independently and almost simultaneously in six regions (Near East, sub-Saharan Africa, China and Southeast Asia, Eastern North America, Mesoamerica and South America), and then spread to become a dominant way of life throughout much of the world.\(^1\) Why did this happen? Arguably no prehistoric question has received more collective scientific attention, and for good reason. Few ‘transformations’ in early hominid history have had a more profound impact than the agricultural transformation.\(^2\)

Understanding the transition from foraging to farming remains a key focus in many disciplines, including anthropology (Bar-Yosef and Meadow 1995), human behavioural ecology (Winterhalder and Kennet 2006), and is one of the major challenges of the emerging field of *paleoeconomics* – the branch of economics studying human behavior in the prehistory (see for example Ofek, 2001; Horan et al., 2005, in press).

The beginnings of agriculture is now recognized to be less about the discovery of cultivation, or overcoming the “complexities” of domestication, than it is about the *level of reliance* on domesticated species. Humans likely discovered seeds as the mechanism for plant growth long before agriculture took root (e.g., Flannery 1968; Cohen 1977). Pryor (2004) reviews evidence suggesting agriculture was relatively straightforward for primitive foragers,

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\(^1\) “Simultaneously” in this context spans a broad range of dates. The origins of farming in the six regions can be traced back to the period 13,000 – 8,000 years ago, which is a long time. But in light of the history of our species, which goes back some 150,000 years, it is remarkably close.

\(^2\) One would be hard to overstate the significance of the agricultural transition. The transition changed the fundamental structure of human society, and laid the foundations for such institutions as centralized government. Researchers argue agriculture is a necessary precursor for the development of social stratification, state-level societies and market economies (e.g., Diamond 1997). Many of the changes brought about by agricultural expansion are related to changes in population densities. While foragers live at densities of about 1 person per 10 square kilometers, densities of rice farmers on Java are 10,000 times higher (Winterhalder and Kennett). The global population ballooned from about 10 million people at the eve of farming to over 6 billion nowadays, and this increase in population density is a major factor in the evolution of institutions and technology (e.g. Kremer 1993, Galor and Weil 1999).
and “proto-plant production” (including the use of fire to encourage new plant growth, flooding fields containing root crops, soil aeration and the broadcast of wild seeds) may have existed for tens of thousands of years prior to the agricultural revolution. Domestication of many grasses is basic (e.g., cereals and rices) and can occur within as few as one to three years (Harlan 1999; Pryor 2004). Rather, Pryor (2004) and Winterhalder and Kennet (2006) define agriculture to be distinct from proto-plant production – agriculture is the near reliance on domesticated species.\(^3\) Winterhalder and Kennet (2006) suggest 75 percent reliance as a criterion (a self-admittedly arbitrary level). Combined with the evidence on early human knowledge and proto-production practices and the ease of domestication for some species, this reliance-based definition suggests the agricultural revolution was the widespread adoption of known practices – a change in behavior – as opposed to a phenomenon of discovery and innovation.

Numerous theories attempt to explain a behavioral transition to agriculture, including those based on (i) technical change that increased the returns to agriculture (e.g. Marceau and Myers 2005; Olssen and Hibbs 2005; Baker 2005; Weisdorf 2003; Rindos 1984; MacNeish 1992; see Kremer 1993 or Galor and Weil 1999 for a more general treatment), (ii) demographic pressure that generated resource pressures and the need to adopt alternative food procurement approaches (Cohen 1977; North and Thomas 1977; Smith 1975), (iii) socio-economic competition and status-seeking behaviors that encouraged the development of surpluses (Haydon 1995), (iv) changes in property rights that gave groups incentives to plant crops for their own procurement (North and Thomas 1977; Baker 2005), (v) increased diet breadth and risk management arising from a co-evolution between human choices, the distribution of wild plant communities across the landscape (Winterhalder and Goland 1997; Winterhalder and Kennett 2006; Piperno and Pearsall 1998; Rindos 1984), and domesticated plants (Rindos 1984), and (vi)  

\(^3\) Both admit at least some agricultural societies did partly depend on hunting.
climate change (Childe 1951; Richerson et al. 2001). Pryor (2004) lists a number of criticisms about applying theories (i)-(iv), and notes that no single theory is likely to provide the sole explanation.

In this paper, we combine elements of three theories—climate change, property rights, and competitive exclusion—to create a paleoeconomic model of agriculture and its diffusion. We focus on climate change as a necessary trigger, which combined with group property rights and competitive exclusion processes produced conditions sufficient for the diffusion of early agriculture.

Our climate change perspective follows Richerson et al. (2001) and Piperno and Pearsall (1998). Piperno and Pearsall (1998, p.27) discuss how easily-domesticable species were in insufficient quantities prior to the Holocene to be a part of human diets. But this story changed in the Holocene as the climate changed. Climate changes, for example caused deciduous forests to replace productive open grassland foraging environments in the lowland neotropics, with more than half of the crops eventually domesticated in the New World coming from these forests (Piperno and Pearsall 1998, p.27). Supporting this view, Richerson et al. (2001) argue climate change would have made domestic production of these new plant options more feasible. Using high-resolution climate proxy data taken from ice cores in Greenland and Antarctica, Richerson et al. (2001) make the convincing argument that agriculture was all but impossible in the Pleistocene. The climate was too cold, too dry, and too variable. In contrast, the Holocene marks a period of warm, wet, and stable climate. The climate change-agricultural diffusion

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4 Rindos’ (1984) discussion of co-evolution, which is somewhat mechanistic and non-optimization-based, differs from human behavioral ecologists like Piperno and Pearsall (1998) and Winterhalder and Goland (1997), who do assume human choices are being optimized.
5 For instance, though rooted in the diet breadth model, human behavioral ecology theories have merged elements of all six theories.
6 Climatic fluctuations during the last 100,000 years of the Pleistocene were extreme – think of annual swings in mean temperature of 10°F. Also, the atmosphere was less rich in carbon dioxide (essential for plant respiration).
theory makes sense if the climatic conditions for farming were only established in the early Holocene and not earlier, if many domesticable plants only became available during this time, and if people already had knowledge of proto-plant production techniques (Pryor 2004).7

Climate change is a necessary but not a sufficient condition, however, for our story to hold; rather we combine climate with property rights and competitive exclusion to develop our theory for agricultural diffusion. Following North and Thomas (1977), we theorize that property rights played an important role. They suggest the common property use of resources under hunting and gathering would reduce the productivity of hunting and gathering, whereas the same would not hold under an agricultural system operated as communal property. Eventually, they claim depletion of common property resources shifted labor allocations to agriculture. North and Thomas state this reallocation of labor does not have to be a conscious process. Rather groups that make more efficient choices will exclude others due to natural selection. But the mechanisms underlying this competitive exclusion process are not formalized. This begs one to ask what competitive forces drive the exclusion process once different groups begin to engage in different activities?

Baker (2005) and Marceau and Myers (2006) develop formal models with private property rights to agriculture, in which the state of technology affects adoption, though neither model explicitly models natural selection. Baker (2005) models advances in agricultural technology as increasing the marginal value of agriculture, which results in more farming activity. But increased farming reduces the amount of land available for hunting and gathering. As agriculture becomes more productive, more land is pulled away from hunter-gatherers who

7 Piperno and Pearsall (1998) note “protracted period of mutualistic interactions between people and the plants taken under cultivation” was not required for agriculture to begin. Some plants would have been easily domesticable in a short time (Harlan 1994).
must be physically evicted for agriculture to spread. Though possible, we believe physical eviction is too strong a requirement for agricultural diffusion.

Marceau and Myers (2006) show how technological change (affecting both foraging and farming) could have increased the chances of coordination failures among large bands of hunter-gatherers who had previously coordinated on conserving behaviors. The coordination failures result in the larger bands splintering into smaller groups who protect their territories, but do not cooperate on conservation. This leads to overexploitation, which increases the relative gains from agriculture. Moreover, increases in agriculture reduce the carrying capacity for wildlife, reducing hunter-gatherer productivity and increasing the relative returns to agriculture. If a selection process of farming over hunting were to arise under this framework, it could be driven by either resource scarcity or changes in land use.

Selection as a result of scarcity of a common resource would be an indirect, ecologically-driven mechanism. Exploring such a mechanism is the third element of our model—the theory of competitive exclusion. Richerson et al. (2001) describe the spread of agriculture as the result of an exclusion process driven by competition for land under competing uses (agriculture versus traditional hunting/gathering). They argue the more efficient regime will generate greater wealth and allow the farmers to take over the land via purchase, warfare, or the submission or flight of hunter-gatherers. Though they do not model these processes formally, Richerson et al. (2001) are describing an exclusion process based on wealth generation and competing land uses, whereby the wealthy farmers physically acquire the land from the comparatively poor hunter-gatherers. Such a mechanism based on direct interactions between hunter-gatherers and farmers is entirely plausible. But we believe it is too strong a requirement and that exclusion can occur
indirectly and under much simpler circumstances based on ecological principles and the basic economic characteristics of the nutritional goods being produced under the two regimes.

Our model of competitive exclusion does not require that land is subject to competing uses, which enables us to discover how agricultural diffusion could proceed under the simplest of circumstances. We assume agricultural lands and wildlife habitat is distinct, and wildlife are harvested as a common property resource. The common property problem arises because harvests occur on common (non-agricultural) lands jointly accessible by either group, or because wildlife populations roam freely across territorial boundaries. Exclusion arises under these assumptions not because of a direct physical eviction, but rather due to an indirect ecological one. Exclusion in our model is consistent with the ecological principle of competitive exclusion – a process by which one species or group replaces a less efficient one via competition for a common resource.  

In ecology, exclusion is at the species or group level, as one group is literally restricted from existence. A similar process arises in economics as more efficient producers out-compete and eventually exclude less efficient producers from the marketplace. But exclusion does not necessarily have to restrict another group from existence. Exclusion can also mean to impose property rights over a resource or good. If the excluded resource is a necessary input into production of another good, an individual or group that claims exclusive ownership over that resource will also be able to exclude competitors from the market – exclusion of the resource implies restricting a competing group from existence. But these types of exclusion – access to a resource versus access to existence – are viewed as different.

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8 Richerson et al. (2001) indicate that opportunistic hunting by farmers could exert additional competition on hunter-gatherers. The implication is this additional competition increases the relative wealth of farmers in their framework. But without a formal model the exact mechanisms at work are unclear.
Herein we show exclusion from a non-necessary resource can lead to exclusion at the group level. Even if farmers are less efficient in the competition for the common property resource, we find they can outcompete the more efficient hunters by spending some time producing from a private property resource. This diversification in production insulates farmers from scarcity in the common pool market. Moreover, if these diversified farmers continue to compete in the common pool market, they can out-compete the more efficient hunters – hunters are competitively excluded in the area where they own the comparative advantage. The model is used to explain humanity’s transition from the hunting and gathering of common property resources to a more widespread adoption of agriculture, an activity in which property rights (at least at the group-level) are fundamental. This includes protection of the group’s land from outsiders, which was common among hunter-gatherer societies (Pryor 2004), and the exclusive use of seed that was perhaps brought in from another region (recall many cultivated crops originated in lowland tropics).

The results of our model are consistent with four stylized facts on the transition to agriculture: (i) the emergence of agriculture coincided with a major change in the climate; (ii) agriculture became the dominant mode of supporting mankind, but its diffusion was neither unidirectional nor encompassing. Periods exist in which ‘farming societies’ like the American Anasazi reversed to foraging, and some societies never adopted agriculture.\(^9\) Also, evidence suggests combinations of foraging and farming can be a stable strategy – the archaeological record suggests that such diversified strategies may have persisted for thousands of years; (iii) diffusion of agriculture was slow, taking thousands of years to reach England from the Middle East. There have been episodes of farming and foraging communities living side by side.

\(^9\) For example, agriculture did not exist in Australia until the 18th century, and hunting-gathering has been dominant in North America for a long time.
(Cashdan 1989); and (iv) agricultural expansion did not necessarily imply replacement of the extant hunter-gatherer population – sometimes hunters ‘switched’ occupation. Other times agricultural expansion replaced or subsumed foraging communities (e.g. Cavalli-Sforza 1996).

A Model of Decision-Making among Hunter-Gatherers and Farmers

We develop a model of two separate groups or populations of primitive people: hunter-gatherers \( (H) \), which we call hunters for simplicity, and farmers \( (A) \). Neither group directly interacts with the other, as both groups are territorial and land used for farming does not reduce the habitats of common pool resources. There is evidence that territorialism arose prior to the development of agriculture, not in response to it (Marceau and Myers 2006). We assume climate change has recently occurred and made agriculture a viable option; we show later how this viability erodes without the productivity enhancements from climate change. Hunting has been the predominant strategy and hunters do not consider farming to be an option. This could be because the hunters’ territory is barren and unamenable to agriculture, they do not have access to the domestic seeds or crops (as many of these were endemic to a only a few areas; Piperno and Pearsall 1998), they lack agricultural knowledge of skill (though this is doubtful; Pryor 2004, Piperno and Pearsall 1998), or due to cultural/religious reasons rooted in the hunting lifestyle.\(^{10}\) Within this framework, we investigate whether a “hunting/farming” or “farming-only” strategy could invade and ultimately replace a system in which the hunting-gathering strategy currently prevails.

\(^{10}\) In reality hunters, either individually or collectively, would make a conscious decision to not farm. Though we do not model this, it could be modeled using the identity model of Akerlof and Kranton (2000). They illustrate how individuals associate themselves with a particular group and how acting against the group generates psychological costs on the individual. Implicitly, we are assuming sufficiently high costs that hunters never switch occupation. It should be noted, however, that over time it may be possible for an individual to change his/her identity (Bulte and Horan 2007), in which case the occupation could change. We mention such a change in our discussion of the simulation results below.
Each population consists of $N_i$ identical households, indexed by $i = H, A$. Both groups sustain themselves by consuming food, denoted on a per capita basis by $F_i$ ($i=H, A$). Hunters consume from a reproducible, common property resource, and farmers may choose to consume from this resource as well. Following Brander and Taylor (1998), we model an aggregate resource stock, $x$, which we refer to as wildlife (though it could include gathered products). Denote the per capita amount that group $i$ consumes from this resource by $m_i$. Agricultural products represent an additional food source, produced and consumed at the per capita level $p_i$. Per capita food intake is defined as $F_i = m_i + p_i$.

Households maximize a utility function, $U_i$, which is a function of food consumption and also a set of other goods like clothes, tools, and shelter, denoted $v_i$.\textsuperscript{11} Utility is defined as:

\begin{equation}
U_i = (m_i + \mu_i p_i)^{\beta_i} v_i^{1-\beta_i},
\end{equation}

which is a hybrid form of Smith (1975) and Brander and Taylor (1999). Each household’s time constraint is given by:

\begin{equation}
l_i = e_i + a_i + y_i,
\end{equation}

where $l_i$ is the total labor endowment, $e_i$ is hunting effort, $a_i$ is effort devoted to agriculture (or gathering), and $y_i$ measures effort to produce other goods.\textsuperscript{12} Assuming constant returns to scale to produce other goods, and we choose units such that $v_i = y_i$.

Agricultural production is represented by $p_i = \mu_i a_i^\eta$, where $\mu_i$ and $\eta$ are parameters.

\textsuperscript{11} Following our earlier work (e.g., Horan et al. 2008) and that of others (e.g., Smith 1975; Brander and Taylor 1998), we continue to assume paleolithic households acted “as if” they maximized a conventional utility function. The model creates a "rational early man" benchmark, which serves to introduce basic economic principles into the general paleontology literature that has traditionally assumed away such basic factors as opportunity costs and tradeoffs.

\textsuperscript{12} We do not explicitly model time required to protect the territory or the decision to do so. Rather, we take as given that members of each group are required to devote some time to protection as a condition of group membership. Therefore, $l_i$ can be viewed as the total time available net of this protection.
meat. Assume agriculture exhibits diminishing returns to labor, i.e., \( \eta < 1 \), as non-labor inputs such as seeds and tools (and weather) represent limiting factors. Hunters do not produce agricultural products; we capture this by setting \( \mu_H = 0 \).

Finally, harvesting of meat is defined by the standard Schaefer production function (Clark 1990):

\[
(3) \quad m_i = q_i e_i x,
\]

where \( q_i \) is the catchability coefficient defining the ease with which wildlife is harvested. Hunters have a larger catchability coefficient than farmers, i.e., \( q_H > q_A \), due to the fact that hunters specialize (developing greater skill) and follow wildlife herds more closely than the more sedentary farmers.

Assume these primitive people solve a series of static labor allocation problems, rather than a single dynamic optimization problem. This presumption is consistent with observations by Mithen (1990, p.224): “hunter-gatherers do not appear to plan subsistence activities over time scales longer than one year.” Our assumption is also consistent with more contemporary instances of open access resource exploitation (see Sanchirico and Wilen 1999; Bulte and Horan 2003). We abstract away from spatial considerations and institutional change that might arise in response to changes in resource scarcity (see Ostrom 1990, Erickson and Gowdy 2000, Pezzey and Anderies 2002).

Substituting the three production relations into (1), the Lagrangean associated with population \( i \)'s problem is:

\[
(4) \quad L_i = (q_i e_i x + \mu_i a_i^\eta) \beta y_i^{1-\beta} + \lambda_i [l_i - e_i - a_i - y_i].
\]

Optimal labor allocations to agriculture and hunting are

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13 A more general specification, albeit analytically less tractable, is the specification \( m = q e x^\varphi \) and \( \varphi < 1 \) (e.g. Henderson and Tugwell, 1979). Our main results are qualitatively robust for this extension.
Hunters always supply $\beta_H l_H$ units of effort to hunting (recall, $\mu_H = 0$). From expression (5), farmers always apply positive levels of effort towards agriculture. In contrast, equation (6) indicates that farmers cease harvesting when the wildlife stock falls below a value of $x_\ast$. These results arise due to constant returns to labor in hunting and diminishing returns in agriculture, which are opposite to the assumptions made by North and Thomas (1979). Full-scale agriculture among farmers results from resource scarcity in our model, but our assumptions actually make it less likely that severe resource scarcity will drive the widespread adoption of agriculture, as was required by North and Thomas (1979) and occurs in Marceau and Myers (2006). The reason is agriculture pulls labor out of the hunting sector, so $x$ is less likely to fall below $x_\ast$.

Equation (6) indicates farmers apply less effort to hunting than hunters. Combined with the smaller catchability coefficient for farmers, this means farmers are less competitive than hunters in terms of per capita consumption of the common property resource, i.e., $m_A^* < m_H^*$, where $m_i^*$ represents the optimal level of per capita meat consumption for group $i$.

Population and Resource Dynamics

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14 Bulte et al. (2006) examine species extinctions in the Pleistocene and find the extinctions likely came from non-selective harvesting of multiple species. They also find that agriculture, if it had existed at the time, could have had a stabilizing effect on resource populations by reducing hunting pressure.
Population growth (or fertility) in both groups depends on the available food supply, which holds for people living close to subsistence (see Frisch 1978; Hansson and Stuart 1990; Nerlove 1991, 1993; Dasgupta 1995). Following conventional models of predator populations (e.g., McGehee and Armstrong 1977), let the dynamics of population \( i \) be described by

\[
\dot{N}_i = N_i (-d_i + b_i F_i (x)) ,
\]

where \( d_i \) is the mortality rate, \( b_i F_i \) is the birth rate, and \( b_i \) is a birth rate parameter. The population shrinks (grows) whenever average household food intake falls short of (exceeds) a subsistence level, \( S_i \).\(^{15}\) The parameter \( b_i \) is set equal to \( d_i / S_i \), where \( S_i \) represents the minimum quantity of food that member of each population need to support themselves. From expression (7), if \( F_i / S_i < 1 \), the population growth rate is negative and the population diminishes. As \( F_i / S_i \to 1 \), the population does not change. If \( F_i / S_i > 1 \), the population grows.\(^{16}\) For simplicity, we drop the subscripts from the population growth parameters and assume they are equivalent.\(^{17}\)

From (5) - (7), we define \( x^*_i \) to be the steady state resource stock that arises when only population \( i \) is present (i.e., when \( N_j = 0 \) for \( j \neq i \)). Define:

\[
x^*_H = S_H / (q_H b_l) ,
\]

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\(^{15}\) Strauss and Thomas (1998) discuss the importance of such thresholds.

\(^{16}\) This specification of population growth is Malthusian in spirit; it presumes caloric intake governs the dynamics – eventually restricting the system to steady states (if they exist) where survival is at the subsistence level. The specification does not address population control, which is a limitation given evidence that contemporary foraging societies make efforts to control fertility. Marceau and Myers (2006) argue that Paleolithic people too controlled their populations, and suggest that various methods population control may have been used including “culturally-demanded abstinence, disruption of the menstrual cycle through extended breast feeding, abortion, direct and indirect infanticide (particularly female infanticide) and even dietary cannibalism.” Examining the consequences of fertility choice is an interesting extension of our model, and one we leave for future work. Such socially coordinated choices suggest a certain level of planning, cooperation and foresight – features not addressed in our model.

\(^{17}\) These assumptions imply that subsistence requirements are identical for both populations. Of course hunters will have different caloric needs than farmers, but the assumption of a common value of \( S \) has little bearing on the results.
whereas \( x_A^* \) is defined implicitly as the solution to

\[(9) \quad F_A(x_A^*) = S. \]

In constructing (9), we assume \( a_A(\hat{x}) < S \); farmers who only practice agriculture cannot sustain themselves. Otherwise, the agricultural population will grow without bound (though wildlife would not necessarily go extinct: see Proposition 3 below). It is reasonable to assume the original farmers would have had to rely on both agriculture and hunting to sustain themselves, particularly prior to the development of animal husbandry which came well after the first domestication of plants (Diamond). The assumption \( a_A(\hat{x}) < S \) also implies \( x_A^* > \hat{x} \), by monotonicity of \( F_A(x) \) for \( x \geq \hat{x} \).

The assumption that agriculture is a less productive activity contrasts with others’ explanations based on technical change as a driving mechanism (North and Thomas 1979; Baker 2005; Marceau and Myers 2006). North and Thomas (1979) do describe one situation in which low productivity agriculture could be adopted, with the impetus being population growth. As we illustrate below, population growth in our model may have a role in the exclusion of hunter-gatherers.

Now consider the ecological side of the model. Wildlife growth is governed by the conventional logistic growth function

\[(10) \quad G(x) = \alpha x (1 - x/k), \]

where \( \alpha \) is the intrinsic growth rate and \( k \) is the carrying capacity. Note \( k \) is unaffected by agricultural production – there is no competing use of the land for agricultural and wildlife production (or hunting). This is a reasonable assumption for many species even today (though many species such as deer and rabbits benefit from agricultural areas), but particularly at the start of the agricultural revolution. Hunter and farmer harvests reduce wildlife growth, and so the
dynamics of the wildlife stock are described by

\[ \dot{x} = \alpha(1 - \frac{x}{k}) - N_H m_H^* - N_A m_A^*. \]

**Competitive exclusion**

Competitive exclusion is the principle that, if two similar species occupy the same niche, only the more efficient survives and the other slowly goes extinct as they compete for resources (McGehee and Armstrong 1977).

**Proposition 1.** If agriculture was not an option for the farmers (i.e., \( \mu_A = 0 \)), then the smaller catchability coefficient for farmers will lead to their extinction, all else equal.

**Proof.** See Horan et al. (2005, Proposition 1).

Proposition 1 implies that would-be farmers, who are less efficient hunters, could not survive as a group if farming were not an option. Farmers cannot survive on either food production activity alone. But how do they fare when both activities are possible? The following Lemma and Proposition address this question.

**Lemma 1:** Assume the groups are identical except that \( q_A < q_H \) and \( \mu_A > \mu_H = 0 \). Also assume \( a_A(\hat{x}) < S \). When agriculture is an option for farmers (with or without property rights), an interior steady state involving hunters and farmers generally will not exist.

**Proof:** See Appendix.
Proposition 2: Assume the groups are identical except \( q_A < q_H \) and \( \mu_A > \mu_H = 0 \). Also assume \( a_A(\hat{x}) < S \). (i) If farmers do not have property rights, they will be excluded by hunters. (ii) If farmers do have property rights over agriculture, farmers will exclude hunters if \( x_H^* > x_A^* \), and hunters exclude farmers if \( x_A^* > x_H^* \).

Proof: See Appendix.

Farmers are not necessarily excluded when agriculture is an option, provided agriculture is an exclusive or private property activity and agricultural productivity is sufficiently great (e.g., as a result of climate change). Three aspects of this result deserve attention. First, we note that farmers’ food consumption meets or exceeds subsistence levels when they partake in both activities, although they are unable to subsist on either resource alone. Subsistence is possible because the marginal productivity of agriculture is initially very high relative to the marginal productivity of hunting. By operating where the marginal productivity of the activities is equal, the farmer can produce more food than could be produced in either activity alone.

Second, property rights are required to generate sufficient agricultural productivity. Property rights over the agricultural resource eliminate competition in this sector that would otherwise reduce agricultural productivity and make it impossible for farmers to invade the system, let alone exclude hunters. Climate change that made agriculture a viable and sufficiently productive option is also required to ensure \( x_H^* > x_A^* \), which is required for farmers to exclude hunters.

Third, property rights over agriculture reduce the ecological effects of competition that farmers face over the common property resource. This effect is key and generates one result that runs counter to traditional models of competitive exclusion. Proposition 2 does not require that
farmers produce more food per capita than hunters, except in equilibrium (see the proof). Rather, farmers can invade the system even when they are producing less food than hunters. The reason is that agricultural food production effectively reduces farmer subsistence levels in the common property resource sector. Farmers need to obtain fewer wildlife harvests to subsist than they would in the absence of agriculture. This lower effective subsistence level improves farmers’ competitive status in the common property sector.

Viewed another way, the private property resource insulates farmers somewhat from the risk of competition involving the common property resource. This response to competitive risk is partly endogenous, as farmers shift some of their hunting efforts towards agriculture as \( x \) falls. Note this shift is the result of resource scarcity only and is not specifically related to subsistence requirements, as \( S \) is not a component of farmers’ utility functions. Protection from competitive exclusion depends on the types of resources being used—private vs. common pool. Previously we illustrated that private property, through its role in exchange of consumption goods obtained from a common pool, can be used to generate surpluses to overcome exclusion pressures (Horan et al. 2005). Now we find private property in production can also protect against exclusion, even in cases in which surpluses do not initially arise. Together these results illustrate how economic systems help to separate humans from nature.

Though individual farmers harvest less meat in a subsistence equilibrium involving agriculture than do hunter-gatherers, the wildlife stock is smaller in the farming equilibrium, i.e., \( x_A^* < x_H^* \). This result can only be explained by a larger equilibrium human population emerging after agriculture. It is impossible to derive an analytical condition to indicate when \( x_H^* > x_A^* \) will hold, due to the highly nonlinear nature of \( F_A \). But the outcome will depend on the relative difference in hunting efficiency between hunters and farmers, and the relative efficiency of
agriculture. If farmers are sufficiently efficient at producing nutrition and if farmers are not much less productive hunters than hunter-gatherers, then $x_{H}^*>x_{A}^*$ will hold and farmers exclude hunters. Otherwise, farming will not take off. One factor that helps explain why agriculture suddenly became viable in the Holocene is climate change that increased agricultural productivity beyond some biological threshold, for instance due to increased CO$_2$ fertilization.

Finally, if agricultural productivity ever did increase to the point in which it was sustainable, it is possible for farmers and hunters to both specialize and co-exist (stylized fact II).

**Proposition 3.** Assume farmers have property rights over agriculture, and the groups are identical except $q_A<q_H$ and $\mu_A>\mu_H=0$. If $a_A(\hat{x}) \geq S$ and $\hat{x}>x_{H}^*$, farmers and hunters will co-exist.

**Proof:** With property rights and $a_A(\hat{x}) \geq S$, farmers can enter the system at any time. They will not hunt, however, as long as $x \leq \hat{x}$. Regardless of whether the initial wildlife stock is large enough to induce hunting by farmers, hunters will eventually depress the wildlife stock to $x_{H}^* < \hat{x}$, at which point farmers no longer hunt and hunters are not excluded.

Using the definition of $\hat{x}$ along with expression (5), we can write $\hat{x} = \mu_A \eta q_{e=0}^{y^{-1}} / q_A$, where $a_{e=0} = \beta \eta l / (1 - \beta + \beta \eta)$ is the effort level that farmers apply to agriculture when they have insufficient incentives to hunt. The condition $\hat{x} > x_{H}^*$ can then be written as

$\hat{x} = \mu_A \eta q_{e=0}^{y^{-1}} / q_A > x_{H}^*$, or

(12) $\mu_A \eta q_{e=0}^{y^{-1}} \geq q_A x_{H}^*$.

Condition (12) states the marginal productivity of agriculture when farmers do not hunt exceeds
the marginal productivity of hunting at the hunter-only equilibrium. For instance, suppose hunters were in equilibrium when a small group of farmers entered the region. The farmers would have no incentive to begin hunting, but instead focus their food production efforts solely on agriculture. The idea here is agriculture is so productive farmers no longer compete in the commons, eliminating the exclusion pressures on hunters.

The notion that highly productive agriculture could ensure the continued existence of hunters is in contrast to North and Thomas (1979), Richerson et al. (2001), Baker (2005), and Marceau and Myers (2006), who suggest that sufficiently great agricultural productivity will always result in the demise of the hunter-gatherer culture. The key to this different outcome is the assumption about land use. We assume agricultural lands and hunting lands are distinct, whereas others assume complete overlap. Reality probably lies somewhere in between, in which case farmers would be able to capture all desirable farmland while leaving some lands available for hunting. If more agricultural land reduces wildlife habitat, the net effect may be to reduce the hunter-gatherer population but not to replace it. Both populations may increase if more agricultural land increases wildlife habitat, though at some point conflict would be more likely.

**Simulation**

We now develop a numerical simulation to illustrate the results. Following Horan et al. (2005) and Bulte et al. (2006), we adopt the following parameter values for a baseline scenario: $k=75$ million AU (1 AU = 1,000 pounds of living animal), $\alpha = 0.15$, $d = 0.08$, $S=2.9$ AU/year, $\beta = 0.6$, $q_A = 8.3 \times 10^{-11}$, $q_A = (1 + \psi)q_A$, $l=7300$, $\eta = 0.45$, $\mu_A = 0.045$, and $\psi = 0.05$. The simulation begins under the assumption that hunters have been in the area for 100 years when a small group of 100 farmers enters the region. At this point, the hunters are not yet in equilibrium with the wildlife.
population. We use an out-of-equilibrium starting point to illustrate how farmers can enter the system while generating less food per capita than hunters. If we instead introduced farmers when the hunters were in equilibrium, then the proof to Proposition 2 indicates that farmers must consume a greater amount per capita to enter the system.

Figure 1 illustrates the population dynamics of the baseline scenario. The farmers can enter the system and they go on to exclude the hunters within about 1700 years. Agriculture may have taken several thousand years to spread, and a combination of foraging and farming could have co-existed during this period (stylized fact iii).\(^{18}\)

Figure 2 illustrates the ratio of per capita food consumption by hunters relative to farmers. We find farmers are able to enter the region and compete for 90 years before they begin to consume more food than hunters. During this time, farmers are producing less than six percent of their food from agriculture – they are primarily inefficient hunters who are able to compete using only a small supply of extra food that does not always increase total supplies above that of the more efficient hunters. It takes 122 years for farmers to be producing 75 percent of their food supplies from agriculture, which is the threshold that Winterhalder and Kennett (2006) define for agricultural societies. This status is short-lived, however. Farmers go through three additional cycles of transitioning from hunters to farmers before they achieve agricultural stability 316 years after entering the region (stylized fact ii).

Table 1 presents our sensitivity results. The results are insensitive to wildlife growth parameters since, from equations (8) and (9), these parameters have no impact on subsistence levels and only affect the total human populations that the wildlife can support. The results are most sensitive to changes in the hunting and agricultural productivity parameters. If hunters are

\(^{18}\) Though we do not model this explicitly, it is also possible that hunters eventually switched to agriculture during this time if they realized their communities were otherwise unsustainable and if they were able to abandon their long-held traditions associated with the hunting lifestyle (stylized fact iv).
ten percent more productive than farmers in hunting wildlife, then hunters cannot be excluded. Farmers must also be sufficiently productive in agriculture. A 13.3 percent reduction in $\eta$ or a 28.9 percent reduction in $\mu$ from their baseline values implies that hunters could then exclude farmers. Alternatively, the interpretation is that even a small (in the case of $\eta$) to moderate (in the case of $\mu$) agricultural productivity-enhancing CO$_2$ fertilization effect in the early Holocene might have tipped the balance in favor of farming (stylized fact i). It is reasonable that both the degree of the fertilization effect and the differences in hunting efficiencies would have differed regionally, meaning that hunting would have persisted longer in some regions than in others.

**Concluding Remark**

We agree with Pryor (2004)—no one theory tells the full story about the transition to agriculture from hunting and gathering. We construct our model based on three separate disciplinary elements: the *geophysical notion* that climate change could trigger a productivity gain that exceeded a minimal biological threshold, the *economic principle* of exchange institutions driven by well-defined private property rights that can trigger needed investments in agriculture resources, and the *ecological idea* of competitive exclusion in which less-efficient farmers out-compete more efficient hunters on common hunting grounds given the farmers first spend time producing additional nutrition from their private property resource. In contrast to the human-dominated technological advancement theories posited in the economic growth literature, our model focuses on the joint determination and interaction between humans and nature and the feedbacks between the two systems. Herein we extend further the endogenous risk idea that society affects nature/nature affects society, which leads us to a theory that could help explain one of the key transition periods in human history—the transformation to agriculture.
In contrast to other models in which farming emerges as technological progress or climate makes it a more productive option than hunting, farming emerges in our model even if farmers are poor hunters and cannot sustain themselves with agriculture alone. Moreover, the strategy of farming can invade the system even if farmers initially generate lower per capita consumption than hunters. The key is that the simple innovation of property rights over an immobile resource can help to insulate farmers from competitive ecological pressures, moving them one small step closer to the modern age in terms of development, but a giant leap away from whence they had been for so long in terms of their role within the ecosystem.
References


Appendix

**Lemma 1:** Assume the groups are identical except that \( q_A < q_H \) and \( \mu_A > \mu_H = 0 \). Also assume \( a_A(\hat{x}) < S \). When agriculture is an option for farmers (with or without property rights), an interior steady state involving hunters and farmers generally will not exist.

**Proof:** For notational convenience, we drop all subscripts except those associated with \( q \) and \( \mu \). Proposition 1, along with the assumption \( a_A(\hat{x}) < S \), indicate that farmers must spend some time hunting to survive in a steady state involving both populations. Consider the case where farmers have property rights. Given that \( S_H = S_A \), equation (7) implies that a steady state involving both hunters and farmers only arises when

\[
(A1) \quad F^*_H = q_H \beta \hat{x}^* = q_A \beta \hat{x}^* + \mu_A \left( \frac{\mu_A \eta}{q_A \hat{x}^*} \right)^{\frac{q}{\nu-\eta}} \beta (1 - \eta) = F^*_A
\]

Here, \( \hat{x}^* \) represents the steady state value of \( x \), which is the solution to (A1):

\[
(A2) \quad \hat{x}^* = \mu_A \left( \frac{1 - \eta}{(q_H - q_A)l} \right)^{1-\eta} \left( \frac{\eta}{q_A} \right)^{\eta}
\]

But, from (7), the steady state wildlife stock must also satisfy \( m^*_H = S \), which yields

\[
(A3) \quad \hat{x}^*_H = S / (q_H \beta l)
\]

where \( \hat{x}^*_H \) is the value of \( x \) that ensures the hunter population attains a steady state. As conditions (A2) and (A3) are both determined by exogenous parameters, the likelihood that \( \hat{x}^* = \hat{x}^*_H \) is essentially zero. A steady state involving hunters and farmers will not exist when \( \hat{x}^*_H > \hat{x} \) and farmers have property rights.

When farmers do not hold property rights, produced crops become available as a common property resource. Hunters can only benefit from this arrangement, while farmers can
only lose. Farmers may have no incentives to grow crops in this situation, which would imply their exclusion. If they did grow some crops, and without specifying the exact nature of the labor allocation problem for this case, a steady state must solve both

\[ F^*_H = q_H \beta l x^* + \Phi_H(x^*) = q_A \beta l x^* + \Phi_A(x^*) = F^*_A \] and \( S = q_H \beta l x^* + \Phi_H(x^*) \), where \( \Phi_H(x^*) > 0 \)

and \( \Phi_A(x^*) < \mu_A\left(\frac{\mu_A \eta}{q_A x^*}\right)^{\gamma} \beta (1 - \eta) \). As above, the system of equations is overdetermined, as a single value of \( x^* \) that solves both equations will not generally exist.

**Proposition 2:** Assume the groups are identical except \( q_A < q_H \) and \( \mu_A > \mu_H = 0 \). Also assume \( a_A(\hat{x}) < S \). (i) If farmers do not have property rights, they will be excluded by hunters. (ii) If farmers do have property rights over agriculture, farmers will exclude hunters if \( x_H^* > x_A^* \), and hunters exclude farmers if \( x_A^* > x_H^* \).

**Proof:** If agriculture is a common property resource, hunters have an evolutionary advantage in both activities, part (i). They are more efficient hunters because \( q_A < q_H \). Hunters would also have an advantage in the agricultural sector because they only have to apply effort to harvesting the crops, while farmers must apply effort to both production and the harvest.

Now suppose farmers have property rights over agricultural resources, part (ii). The definition of \( x_i^* \) implies \( F_i(x_i^*) = S \) for each \( i = A, H \). Note \( F_i(x) \) is monotonically increasing in \( x \) (for all values of \( x \) when \( i = H \), and for \( x \geq \hat{x} \) when \( i = A \)). Consider the case where \( x_H^* > x_A^* \) (the proof for the other case is analogous, so we do not spend time on it here). From Lemma 1, there is no interior equilibrium involving both populations. The dynamics of the system are
governed by the corner equilibria of hunters-only \( (x = x^*_{H}, N_H = N^*_H, N_A = 0) \) and farmers-only \( (x = x^*_A, M_A = M^*_A, N_H = 0) \).

First consider the hunter-only equilibrium. Farmers can only enter the system if their production of food at the hunter-only equilibrium exceeds their subsistence level, i.e.,

\[ F_A(x^*_H) > S. \]

Given that \( S \) also equals \( F_A(x^*_A) \),

(A4) \[ F_A(x^*_H) > F_A(x^*_A) \]

This condition is only satisfied when \( x^*_H > x^*_A \), by monotonicity of \( F_A \). Prior to this invasion, hunters would be consuming at their subsistence level. When farmers invade the system, \( x \) falls and hunters will consume below their subsistence level, resulting in \( \dot{N}_H < 0 \). Alternatively, \( \dot{N}_A > 0 \) as long as \( x \) remains greater than \( x^*_A \).

Now consider the farmer-only equilibrium. Hunters cannot enter the system if their production of food at the farmer-only equilibrium is less than their subsistence level, i.e.,

\[ F_H(x^*_A) < S. \]

Given \( S \) also equals \( F_H(x^*_H) \), we have

(A5) \[ F_H(x^*_H) > F_H(x^*_A) \]

As above, this condition is only satisfied when \( x^*_H > x^*_A \), by monotonicity of \( F_H \). When \( x^*_H > x^*_A \), farmers exclude hunters: farmers invade and out-compete the hunters, whereas hunters cannot invade.
Table 1. Sensitivity Analysis

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value at which hunter-gatherers exclude farmers</th>
<th>Percentage change from baseline</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
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<td>$\text{---}$</td>
</tr>
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<td>$k$</td>
<td>$\text{---}$</td>
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</tr>
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<td>$S$</td>
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<td>$\psi$</td>
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</tr>
<tr>
<td>$\mu$</td>
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<td>-28.9</td>
</tr>
</tbody>
</table>

* A percentage change is not reported for $\psi$ because $\psi$ already represents a percentage change in the hunting productivity differential between hunters and farmers.
Figure 1. Exclusion of hunter-gatherers under the baseline scenario
Figure 2. The ratio of hunter-gatherer food consumption to agricultural food consumption over time